INTRODUCTION

As a natural outgrowth of a revisionary study of the genus *Mesoplodon* of the beaked whale family, Hyperoodontidae,[1] toward which I have been working for several years (Moore and Wood, 1957; Moore, 1958, 1960, 1963b, 1966; Moore and Gilmore, 1965) it has recently been possible to devote a little time to seeking out and testing diagnostic characters of the other genera of the beaked whale family. That some diagnostic characters are badly needed is indicated, for example, by a beaked whale from the Scottish coast reported to be *Mesoplodon mirus* (Stephen, 1931) because its teeth were laterally compressed (Fig. 1, right), but, on checking its nasal bones in October, 1963, at the Royal Scottish Museum, I found it to be *Ziphius cavirostris*. Similarly, Mousset and Duperier (1956) reported at length upon the first *Mesoplodon mirus* from the coasts of France, but their published photographs of the skull of their specimen showed it to be *Ziphius cavirostris*. A *Ziphius cavirostris* 28 feet long was reported by the late A. C. Stephen (1932, pp. 164–166, fig. 2) who illustrated it by a photograph of its teeth which, like its body length, are those properly of *Hyperoodon ampullatus* (Fig. 1, center).

The urgent need of diagnoses for the hyperoodontid genera of whales is sharply indicated by two papers by McCann recently published in New Zealand. One of these McCann (1962b) devoted to removing the species *Mesoplodon hectori* (Gray) 1871, from the genus *Mesoplodon* and recognizing it as the young of a different genus and species, *Berardius arnuxi*, which otherwise ". . . is *only* known from adults!" (Italics and exclamation point McCann's, 1962b, p. 84.) In consecutive pagination with that, McCann (1962c) published another paper devoted to removing the species *Mesoplodon pacificus* Longman, 1926, from the genus *Mesoplodon* because he had formed the opinion that the one known specimen of *pacificus* (a skull) must be the female of a different genus and species, *Hyperoodon planifrons*,

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[1] After Gray (1866, p. 62) used the name Hyperoodontidae for the beaked whale family in listing the families of whales, he (*op. cit.*, p. 326) noted the priority of its type genus and then rejected it in favor of Ziphiidae for further use in that work and later ones, on grounds not acceptable today by the International Rules for Zoological Nomenclature (inadvertent use of prefix hyper instead of hypo).

the skull of which he thinks might be otherwise unknown. These two proposals were made by an elderly naturalist with a long museum background who has had the world's second largest collection of the family Hyperoodontidae to study and has been publishing notes on them. Whatever their merits, these two propositions, like the misidentifications mentioned above, demonstrate that the genera of living beaked whales need diagnoses.

In his most recent classification of the Mammalia, Simpson (1945, p. 215) has pointed out that for the beaked whale family, "No good grouping of the genera within the family has yet been achieved." Fraser and Purves (1960, fig. 26) describe a complex of new morphological characters related to hearing in the Cetacea, and checking the osteological characters out through examples of 34 genera, offer a modified classification of the Cetacea to the generic level. This has contributed some interesting changes from the synthesis offered by Simpson (1945), but in the beaked whales it has principally restored them to superfamily status. Fraser and Purves employ a substantial number of morphological characters, mark which of these applies to each genus in the Cetacea, and enumerate the sample examined for each. Other recent authors offer: 1) a spare and preliminary checklist of marine mammals (Scheffer and Rice, 1963), emerging less from study of specimens than the literature; and 2) a catalog of the Cetacea (Hershkovitz, 1966) resulting from a nearly exhaustive compilation of the literature, with special effort on the synonymies and distribution records. Although Scheffer and Rice (1963) cite a number of 1961 papers and Hershkovitz (1966) had ample time to consider the changes introduced by Fraser and Purves (1960, fig. 26) into Cetacean classification, neither of these latest compilations utilized the changes by Fraser and Purves to the extent that I believe would have improved their works.

State of Knowledge

The ordinary scientific paper published on one of these whale species of little or no commercial value, usually emerges from a study of a single specimen. Often no other pertinent specimens are accessible to the author, and comparisons may only be made between his specimen and what is in the literature. Despite the well-developed custom that an author publish many measurements and drawings or photographs of such a whale specimen and substantiate identification by comparison with earlier publication, the new knowledge contributed by any one such paper is almost exclusively descriptive anatomy

FIG. 1. Left to right in both a and b: *Ziphius cavirostris* (FMNH 95286) ♀ from Puerto Rico, 2 teeth; *Hyperoodon ampullatus* (RSM) ♂ from Huxter (originally misidentified as *Ziphius cavirostris*, see text), 2 teeth; *Z. cavirostris* (RSM) ♀ from Geirnish, originally misidentified as *Mesoplodon mirus*, 2 teeth; Posterodorsal view (a), left lateral view (b).

and geographic distribution. The more measurements made carefully in the manner utilized by earlier authors, the better the contribution toward future knowledge of taxonomic relationships, of sexual dimorphism, of geographic variation, of individual variation, and of ontogenetic variation (see Norris, 1961). Only occasionally is it possible for such a paper to contribute successfully to taxonomy by a suggestion that one or more of the characters described appear to distinguish this species from one or two other species, or to be diagnostic for the species or genus.

Individual variation remains virtually unexplored, and ontogenetic changes have been described in but a few species (e.g., *Ziphius cavirostris* by Kernan, 1918; *Mesoplodon europaeus* by Rankin, 1956). Sexual dimorphism is known to exist for *Berardius bairdi* and *Ziphius cavirostris,* for females of both species are shown to be larger by Omura, Fujino, and Kimura (1955). Certain characters of the rostrum and the teeth of *Ziphius* are shown by True (1910, p. 54) and by Fraser (1942), to attain strikingly different development in males than in females. Direct detailed comparison of several skulls of adult males with several of those of adult females has not been attempted in most other species of beaked whales for lack of availability of such samples. Basic knowledge has, therefore, not been adequate for as fully detailed diagnoses as one would prefer to be able to present for a contribution to the relationships within the genera of living Hyperoodontidae.

A principal difficulty facing anyone attempting to diagnose beaked whale genera, furthermore, is the large number of poorly known species in the genus *Mesoplodon* and the fact that this genus stands unrevised. The genus *Mesoplodon* is not heretofore known to have any single characteristic common to its living species that in fact distinguishes *Mesoplodon* from all the other living genera of beaked whales. Thus, one could not ascertain whether a feature found to be characteristic, say, of *Ziphius* distinguishes it from the living species of *Mesoplodon.*

SCOPE

The present paper seeks to provide a means for confident identification of beaked whales that will be both easier and more complete than presently exists, and will, therefore, enable each zoologist to publish his own observations on the specimen of some rare species found, perhaps once in a man's lifetime, at the seashore. It seeks also to reveal to the naturalist or zoologist an idea of what some details of importance are which are yet unknown (by frequently offering in detail how much *is* known, or from how few specimens) so that one can see at least a place at which to begin to dispel the world's ignorance about the species of the specimen he has found.

Although begun primarily with the above purpose in mind, this paper has grown in scope during the writing of it, principally in the presentation of the discoveries of new taxonomic characters (by which the improved keys and diagnoses are made possible), and the interpretation of their probable value to recognizing and expressing the different degrees of relationship of the genera to each other. This became the major goal of the paper.

In presenting the evidence from position, size, and shape of the teeth, preparatory to offering a classification of the living genera of beaked whales, I recognized a correlation among the males of the species of *Mesoplodon* between location of tooth, posture of tooth, and location of the denticle on the tooth. This is included as the basis for a classification of the living species of *Mesoplodon*, originally not regarded as within the scope of the present work.

MATERIALS

Investigation of the following numbers of skull specimens of the genera *Berardius*, *Ziphius*, and *Hyperoodon* for characters which distinguish them from each other and from *Mesoplodon* and *Tasmacetus* was undertaken between September 1963 and March 1964 at the following institutions. This by no means all of the specimens at every institution listed, for on many occasions I had only time to study the available *Mesoplodon*. For kind permission to study these materials I am indebted to the following indicated officials. The letters topping the columns are initials of the genera. Initials in bold face are those used in text and caption references to specimens identified by catalog numbers.

B	Z	H	M	T	
4	12	4	27	–	British Museum (Nat. Hist.), London, Dr. F. C. Fraser, Miss J. E. King
7	10	1	14	–	United States Nat. Mus., Washington, Dr. D. H. Johnson, Dr. C. O. Handley
4	9	–	16	1*	Dominion Mus., Wellington, N. Z., Dr. R. A. Falla, Mr. Charles McCann
–	2	–	13	–	American Mus. Nat. Hist., New York, Dr. H. E. Anthony, Dr. R. G. VanGelder

* Only a mandible.

B	Z	H	M	T	
1	1	6	6	–	Univ. Zoologiske Mus., Copenhagen, Dr. F. W. Braestrup
–	1	3	9	–	Royal Scottish Mus., Edinburgh, Dr. A. S. Clarke, Mr. A. R. Waterston
–	–	6	6	–	Rijksmuseum van Natuurlijke Hist., Leiden, Dr. D. A. Hooijer
1	1	1	8	–	South AUstralian Mus., Adelaide, Dr. W. P. Crowcroft
2	1	–	7	–	Otago Museum, Dunedin, N. Z., Dr. R. R. Forster
1	1	1	5	–	Mus. National d'Hist. Nat , Paris, Dr. J. Anthony
1	2	–	4	1	Wanganui Public Mus., Wanganui, N. Z., Mr. A. J. Bannister
–	1	2	4	–	Inst. Royale Sci. Nat. Belgique, Brussels, Dr. X. Misonne
–	1	–	6	–	Australian Mus., Sydney, Mr. B. J. Marlow
–	–	–	6	–	South African Mus., Capetown, Dr. F. H. Talbot
1	2	–	2	–	Auckland Inst. and Mus., N. Z., Dr. A. W. B. Powell
1	–	–	4	–	The Museum, Port Elizabeth, S. Africa, Miss R. M. Tietz, Dr. E. R. McLachlan
–	–	–	5	–	Mus. of Comparative Zool., Cambridge, Mass., Mrs. B. L. Schevill, Mr. W. E. Schevill
–	1	–	4	–	Queensland Mus., Brisbane, Mr. Alan Bartholomai, Mr. Jack Woods
–	–	–	5	–	Western Australian Mus., Perth, Dr. W. D. L. Ride
1	–	–	3	–	Mus. of Vertebrate Zool., Berkeley, Calif., Dr. S. B. Benson
–	3	–	1	–	National Mus. of Ceylon, Colombo, Dr. P. E. P. Deraniyagala
–	–	–	2	1	Univ. of Canterbury Mus., Christchurch, N. Z., Dr. B. Stonehouse
2	–	–	1	–	National Sci. Mus., Tokyo, Dr. Yoshinori Imaizumi
1	–	–	3	–	Univ. of British Columbia Mus., Vancouver, Dr. I. McT. Cowan
–	–	–	2½	–	Oxford Univ. Mus., England, Dr. A. J. Cain
–	–	–	2	–	Acad. of Natural Sci., Philadelphia, Mr. Robert R. Grant
–	–	–	2	–	Bernice P. Bishop Mus., Honolulu, Hawaii, Mr. Edwin H. Bryan
1	–	–	1	–	California Acad. of Sci., San Francisco, Dr. R. T. Orr
–	–	–	2	–	Canadian National Mus., Ottawa, Mr. Phillip M. Youngman
–	–	–	2	–	Nat. Mus. of Victoria, Melbourne, Australia, Mr. R. Mark Ryan
–	–	–	2	–	North Carolina State Mus., Raleigh, Mr. Harry Davis
–	–	–	2	–	Southern Illinois Univ., Carbondale, Dr. E. C. Galbreath
–	–	–	2	–	Zoologische Museum, Amsterdam, Dr. P. H. van Bree
–	–	–	1	–	Whales Research Institute, Tokyo, Dr. M. Nishiwaki
–	–	–	1	–	Charleston Mus., South Carolina, Mr. E. Milby Burton
–	–	–	1	–	Southland Mus., Invercargill, N. Z., Mr. Gordon White
–	–	–	1	–	Tasmanian Mus., Hobart, Dr. Eric R. Guiler
–	–	–	1	–	Univ. of Alaska Mus., College, Dr. L. J. Rowinski
–	–	–	1	–	Univ. Oregon Mus. Nat. Hist., Eugene, Dr. J. A. Shotwell
–	–	–	1	–	Yale Peabody Mus. Nat. Hist., New Haven, Conn., Dr. A. W. Crompton
1	–	–	–	–	Provincial Museum of British Columbia, Victoria, Dr. G. Clifford Carl
1	–	–	–	–	Burke Mus., Univ. of Washington, Seattle, Dr. Walter A. Fairservis
–	2	1	–	–	Field Museum of Natural History, Chicago

PROCEDURE

At the United States National Museum I compared a synoptic series of skulls of the living species of beaked whales available, for measurable or describable differences that might prove diagnostic. These differences, carefully defined in writing with constant reference to the specimens, were taken to the storage places of the other specimens of living genera of beaked whales and tested against ten of the examples of *Ziphius* and all of the other specimens. Any of these supposed generic differences that did not distinguish every specimen of the appropriate genus from every specimen of at least one other genus, was discarded. A record sheet kept for each of the surviving, tentatively generic characters showed how many specimens in the museum it distinguished of the diagnosed genus, and from how many of each other beaked whale species each character did, *and* did not, distinguish the genus in question.

At the British Museum (Natural History) the whole process was repeated. A number of new presumably diagnostic characters were found, and all were tested there on the largest collection of forms of living beaked whales in the world. At the other museums listed above, then, the remaining characters that were still potentially diagnostic were further tested and the record kept on the specimens enumerated above. It was not until near the end of this trip that I studied the only three extant specimens of the genus *Tasmacetus*. The characters being tested for diagnosing the other genera were tested on these specimens of *Tasmacetus*, of course, but characters observed in *Tasmacetus* could not be tried out on more than the few specimens to be examined on the remainder of the trip. This explains the limitation of the diagnosis of *Tasmacetus* to one character.

The taxonomic characters so gathered and tested included many which proved to distinguish one genus from one, two or three, but not all, other genera. In the present paper the only generic characters used are those considered to distinguish one genus from adults of all living species of every other genus of the family. Restriction of this study to characters of the skull is in a sense regrettable, for some probably good characters of the postcranial skeleton have been pointed out in the literature. This restriction was dictated by scarcity of time. (A number of other museums were visited where no time at all was available for study of either skulls or postcranial skeletons of genera other than *Mesoplodon*.) Also, the total sample of skulls available in museums far exceeds that of the postcranial skeleta, and is thus far more suitable for quantitative testing of taxonomic characters. Few are the provincial museums, indeed, which will collect and store more than one whole skeleton of a species of whale, but many will make room for two or three, or a half dozen, skulls of a small species of whale reputed to be rare or especially interesting.

Criteria of Adulthood and Sex

It is a common practice among mammalogists to regard a mammal as morphologically adult when the epiphyses have become so fused to the centrum of each of the vertebrae that their sutures are obliterated. As indicated just above, it is seldom that the vertebrae of a beaked whale may be examined to provide this criterion. For the same reason it is also a common practice among mammalogists studying large numbers of other, even mouse-size, mammals for which it has not been convenient to collect the postcranial skeleton, to seek therefore some other criterian of adulthood. I have used the filling of the pulp cavity at the base of the tooth as a criterion of adulthood.

One indication that this may be even more conservative a criterion of morphological adulthood than the obliteration of epiphyseal sutures is the female *Ziphius* FMNH 95286 (see lower middle pair of teeth in fig. 5). Although the pulp cavities are not completely filled (3 x 4½ mm. wide; 6 mm. deep) on each of her teeth, the epiphyses of the cervical, caudal, lumbar, and thoracic vertebrae are so entirely ankylosed to their centra that the sutures are obliterated. Also, the epiphyses at each end of the humerus, radius, and ulna so fused that the sutures are obliterated. No quantitative study in the Hyperoodontoidea on the relationship of the closure of the pulp cavity of the tooth to obliteration of the epiphyseal sutures presently exists.

Preserved sex organs of beaked whales are far scarcer even than postcranial skeleta, and criteria for determination of sex would have been more of a problem had not the scanty positive evidence in the literature suggested use of the strong sexual dimorphism in the teeth and in the degree of filling of the mesorostral canal. Then Nishiwaki and Kamiya (1958) found that their type specimen of *Mesoplodon ginkgodens,* although putatively a male because the teeth were large and erupted, and adult because the epiphyseal sutures of the vertebrae were obliterated, nevertheless had a nearly empty mesorostral canal. This variant from the consistent record that specimens otherwise established to be adult males of *Mesoplodon* had the mesorostral canal filled to the brim with bone in at least the posterior fourth of the canal length, cooled one's enthusiasm for that character as a sex criterion.

I have continued with the working hypotheses accepted earlier (Moore, 1963b, pp. 398, 415) that until evidence emerges to the contrary: 1) Teeth with filled or virtually filled (as FMNH 95286 above) pulp cavities provide a criterion of adulthood. 2) Teeth exhibiting natural wear as evidence of having erupted in life are a criterion of male sex. 3) Teeth exhibiting no such wear but with pulp cavities completely or virtually filled are a criterion of female sex.

Other evidence *is* sought, of course, constantly testing these working hypotheses and should be reported elsewhere for *Mesoplodon*. When one examines specimens with teeth, which by these criteria represent both sexes of a single species, it is also an acceptable working hypothesis that the male teeth will be larger than the female ones (hence the mouth of the alveolus will be larger in males of the species of *Mesoplodon*). In the present paper evidence is offered (Table 1) that *Hyperoodon ampullatus* may be an exception to this working hypothesis regarding size of teeth.

THE STATUS OF *Mesoplodon hectori*

At the present writing (January, 1967) the species *Mesoplodon hectori* is known from but three specimens, two in the British Museum (Natural History), London, and one in the Dominion Museum, Wellington, N. Z. All of these are represented by nearly whole skulls, but all are evidently of individuals that were immature. I have studied these specimens comparatively, each in the presence of what was (1963–64) one of the world's two largest collections of the beaked whale family, and took more than 50 measurements of each specimen. The measurements have now been plotted on graphs for comparing them with the same measurements for the other 11 species of the genus *Mesoplodon*. The detailed results of the above study will emerge in a revision of the genus *Mesoplodon*, but some reference to them seems necessary here because they bear on the generic relationships of *hectori*.

Allegation

As mentioned above, one writer has published an opinion that the specimens recognized by other recent authorities as *Mesoplodon hectori* actually represent the otherwise unknown young of another genus and species of beaked whale *Berardius arnuxi* (McCann, 1962b). The species *Berardius arnuxi* is represented in the Dominion Museum, where McCann worked, by four skulls. I found time to make detailed study of these and nine more skulls in other museums, as well as of ten skulls of the only other species of *Berardius* (which is evidently so similar that the status of the two as different species is not well established. (See Pike, 1953; Slipp and Wilke, 1953.) Thus, I have studied intimately and comparatively the skulls of at least 23 pertinent specimens of *Berardius* as listed on pp. 213, 214, and am working with the skull characters of a much larger sample than that of any previous author.

As a basis for removing *hectori* from the genus *Mesoplodon*, McCann (1962b, p. 83) states that *hectori* does ". . . not conform to the strict definition of the genus [*Mesoplodon*] in several details." as follows:

(a) "The most important [of these] . . . [is] the symmetry of the skull. . . ."

(b) "Another . . . is the absence [in *hectori*] of definite maxillary tubercles and notches [presence of which is] . . . a marked feature of the genus *Mesoplodon*."

(c) "In *M. hectori* in place of the maxillary tubercle there is a maxillary crest; . . . a feature of *Berardius*."

(d) McCann (1962b, p. 89) considers ". . . the three specimens of *M. hectori* to be neonatals or near neonatals. They are too large for any species of *Mesoplodon* and therefore . . . must be regarded as young of some other ziphioid whale such as *Berardius*."

(e) "The single mandibular tooth *only* in each ramus [of] the three specimens of *Mesoplodon hectori* . . . may be accounted for . . . [as] non-development of the posterior tooth [characteristically developed in *Berardius*] at such an early age or its loss by masceration . . . the anterior tooth alone is sometimes erupted in *Berardius* (Dom. Mus. 7)."

(f) ". . . the posterior extremities of the premaxillae in the genus *Mesoplodon* tend to turn outward. . . . This is not the case in *M. hectori* . . . the extremities are more or less symmetrical."

(g) In ". . . adults of *Mesoplodon* . . . the nasals do not overtop the extremities of the premaxillae, but in [*Berardius*] the nasals overtop the premaxillae. In . . . *Mesoplodon hectori* the former condition prevails, but this is undoubtedly . . . due to immaturity."

(h) The ". . . character of paramount importance is . . . a 'blind pit' in the posterior wall of the narial passage, one on either side of the narial septum . . . present in the genus *Berardius* only . . . of the

Ziphiidae. This 'pit' is present in specimens of *Mesoplodon hectori* [pl. 1]. . . ."

Evaluation

In the following comments reference is made to illustrations already available in the literature at the time McCann (1962b) wrote rather than by providing new illustrations here for the greater convenience of the reader but which McCann could not then have seen.

(a) The asymmetry of the known skulls of *Mesoplodon hectori* is in fact quite as great as that of *Mesoplodon grayi* and *M. mirus,* for example. Compare dorsal views of the skulls of *hectori* in Fraser (1950, pl. 3, fig. 1) and McCann (1962a, pl. 2, upper) with those of *grayi* in Forbes (1893, pls. 12, 13), Hale (1932, fig. 2), or Brazenor (1933, pl. VI, right), and then of *mirus* in Raven (1937, fig. 9), Thorpe (1938, pl. 1), or Harmer (1924, pl. 1).

(b) By "absence of definite maxillary tubercles and notches" McCann evidently (see Harmer, 1924, text fig. 3, mx.t.) means maxillary prominences in the terminology of Fraser (1955, p. 625) and prominential notches in that of Moore (1963b, fig. 14) who illustrates both. The former feature is seen to be no better developed in *Mesoplodon stejnegeri* and *M. grayi* than in *hectori* in the above cited photographs of the dorsal view of skulls of *hectori* with those of *stejnegeri* in True (1910, pl. 3) and of the type of *hectori* shown on one plate with three specimens of *grayi* by Flower (1878, pl. 71). Similarly, the notch is present but faintly expressed in all three of these species, in *stejnegeri* quite as faintly as in *hectori.*

(c) No difference is seen between the maxillary "tubercle" of *Mesoplodon* and the maxillary "crest" of *Berardius* fundamental enough to warrant recognizing these structures by separate names in these two genera. The same prominence is present in *Ziphius* and *Tasmacetus* also, but in the living genera of beaked whales only the enormous maxillary crests of *Hyperoodon ampullatus* represent an example of development extreme enough of these same maxillary prominences to warrant recognition of these structures by a separate name. *M. hectori* does in fact have a maxillary tubercle (= maxillary prominence) and is, as shown above, not different from some other species of *Mesoplodon* in this.

(d) It is true that all three known specimens of *M. hectori* are of immature individuals, but they are obviously of three different stages of development, as shown by the skull measurements in McCann's

(1962b, p. 92) own table, and in my opinion only the smallest need be regarded as approximating size at birth. Far from their being "too large for any species of *Mesoplodon*," even the largest specimen of *hectori* has a greatest length of skull, and greatest breadth of skull, smaller than that of any adult that I have measured of any species of *Mesoplodon*. Thus, the known specimens of *hectori* are small enough to be the young of even the smallest species of *Mesoplodon*.

(e) Because in *Berardius* the apical teeth of adults have shallow alveoli, as will be described below, the considerable depth of the alveolus of *hectori* shown by McCann's (1962b, p. 88, pl. 3, fig. 6) own drawing strongly suggests that any posterior tooth "lost by masceration" would have left an alveolus. If these specimens of *hectori* did represent young of *Berardius*, then the alveolus would become relatively shallower during ontogeny, and an alveolus should be present for the posterior tooth in immatures.

Kirino (1956) studied variation in number of teeth of *Berardius bairdi* and in carefully obtaining and studying teeth of 65 specimens reported all variations in number to be greater than the ordinary four. To infer that by chance of individual variation all three of the small young of *Berardius arnuxi* now known have but two teeth each seems most extreme.

(f) That the posterior extremities of the premaxillae do in fact expand laterally (or "dilate laterally" as Flower, 1872, p. 209, puts it) may easily be seen in Fraser's (1950, pl. 3, fig. 1) illustration of the skull of the ontogenetically oldest individual. It is true that *hectori* does this less than any other species of *Mesoplodon*, but it is also true that *hectori* resembles some species of *Mesoplodon* more closely in the degree of this lateral dilation than it resembles any *Berardius*. This was, of course, evident to me in examining the same specimens that McCann had published upon, and will be evident to persons familiar with *M. grayi* from figures in Flower (1878, pl. 71), or Forbes (1893, pls. 12, 13) who look at Hale's (1962, pl. 5b) photograph of *Berardius arnuxi* and Fraser's (1950, pl. 3,1) of *hectori* as well as McCann's (1962b, pls. 4, 5) illustrations.

(g) The pre-eminence of the premaxillaries over the nasals on the vertex of the skull distinguishes *hectori* as *Mesoplodon* not *Berardius*. To try to explain this away in *hectori* by the immaturity of the specimens, is but rationalization in the psychological sense.

(h) This is an assertion without quantitative support, and neither McCann nor I have gathered data on it to determine to what extent it may resemble a taxonomic character. The importance which McCann attributes to it has therefore not been demonstrated.

As for the allegation quoted in my introduction that, "*Berardius arnuxi,* although . . . known for over a century is *only* known from adults"—it is noted that the Dominion Museum, where McCann wrote, has besides four skulls of *B. arnuxi,* catalogued sets of teeth of eight other individuals of *B. arnuxi.* Regarding one of these my my notes say, "D. M. no. 526 [from] Pencarrow, New Zealand, by J. Bollons, purchased 11 August 1931, apical pair of teeth. Pulp cavity open 0.95 of root length, maximum [width of opening] 2 to 3 mm." No evidence is known to me that would cast doubt on an identification of DM 526 as a quite immature specimen of *B. arnuxi.*

The above indicates that however sincere McCann (1962b) may be in his concept of *hectori* representing in fact the young of *Berardius,* he has not succeeded in being objective in his observations (a), (b), (c), (d), (e), and (f), and he musters no clear evidence that his concept is correct. Objectively recorded evidence reported in the present paper from the largest samples of *Berardius* and *Mesoplodon* skulls ever studied, reveals that *hectori* belongs to the genus *Mesoplodon.* Consequently *hectori* is treated as a species of *Mesoplodon* in the diagnosis and classification which follow.

The Status of *Mesoplodon pacificus*

Described in 1926 from the skull and jaw of a single adult specimen found on the beach over 80 years ago, and still known from that specimen alone, *M. pacificus* already has a reputation as a species that invites ill-founded speculation. I disposed (1960, p. 26) of a too conservative earlier allegation that *pacificus* is but a large subspecies of *Mesoplodon mirus*[1] and must now deal with a too radical allegation that it is a female *Hyperoodon planifrons.*

Allegation

McCann (1962c) provides the following items as evidence that the type specimen of *Mesoplodon pacificus* is "an example of the hitherto

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[1] It is not intended here to disparage the first conjecture (by Raven, 1937 pp. 22–25) through this association with the second. Raven's (1937) paper vastly increased the knowledge of two species of *Mesoplodon,* and the number (1) of specimens of *mirus* available to him did not define its characteristics so authoritatively as did the number (7) available to me (1960). The second conjecture (by McCann, 1962c) seems, however, to have been published solely as a paper of conjecture.

unrecognized female of . . ." *Hyperoodon planifrons:*

(a) ". . . dimensions of the . . . skull of *M. pacificus,* particularly . . . the cranial region, exceed those of any known species of *Mesoplodon* very considerably. . . ."

(b) "The great length of the symphyseal union."

(c) "The size [sic] and shape of the alveoli indicate *circular* or *oval* cross-section and not the strongly, *laterally* compressed teeth of . . . *Mesoplodon* . . ."

(d) "The character and position of the lacrimal . . ."

Evaluation

To the above propositions, objection may be made as follows:

(a) While the skull of *pacificus* is shown to be substantially larger than any other species in my unpublished measurements of *Mesoplodon,* the next largest species, *M. layardi,* exceeds the remainder by proportional amounts, and the next largest still, *M. carlhubbsi,* is proportionally larger than the remainder by almost as many measurements. In *Physeter catodon* the size of the adult male exceeds that of the adult female of the same species to this same extent. Thus, for difference of this extent in overall size to be accorded generic significance would split the genus *Mesoplodon* excessively, and as will become apparent in this paper, mere size need not be considered a generic character of primary importance in this family, if, indeed, it should be in any.

(b) The length of the mandibular symphysis (317 mm.) in *pacificus* is in fact not great for *Mesoplodon.* Five specimens of *layardi* and five of *grayi* that I have measured possess longer symphyses than that of *pacificus* (three of these are nos. 714, 1079, and 1379 in the Dominion Museum where McCann worked). Since both *layardi* and (especially) *grayi* have shorter mandibles than *pacificus,* many more specimens of *layardi* and *grayi* and some of *Mesoplodon bidens* must obviously have proportionately longer symphyses.

(c) The greatest width and length measurements of the alveolus of *pacificus* are respectively 18 and 30 mm., a compression ratio of 0.60 (Longman, 1926, p. 269, gives 17 and 28 mm., respectively). This does not suggest a shape very much more rounded than that found in cross-sections of some teeth of *Mesoplodon;* where the compression ratio reaches above 0.58 in teeth of two specimens of *M. mirus* and as high as 0.56 in *M. densirostris.*

(d) The somewhat abraded lateral exposure of the lacrimal is distinctively shaped in *pacificus,* but no more so than is that of *Mesoplodon mirus.*

McCann (1962c, p. 97) cites a letter in the Dominion Museum files written to W. R. B. Oliver by Longman (some ten years after Longman had published the *original* description of *Mesoplodon pacificus*) stating that the specimen of *pacificus* was too much abraded in two areas for original margins of certain bones to be traced. McCann exaggerates this and proceeds then erroneously to assume that virtually all of numerous and impressive differences between Hale's (1931, p. 295) photographs of an adult male skull of *Hyperoodon planifrons* and Longman's (1926, figs. 1–3) of the type of *M. pacificus* that cannot be attributed to sexual dimorphism are results of this abrasion.

Mr. McCann had never examined the type (and only) specimen of *M. pacificus,* but in January 1964 I took 54 measurements of it, recorded many more observations on it, and checked *upon the specimen* every statement of Longman's original published description.

No error of significance was discovered. I carefully studied the abrasion of the type of *pacificus* and concluded that serious change of the shape of the skull by abrasion was restricted to its vertex which looked as if the person who found it might have dragged it on the sand a distance with the vertex down, abrading it to a depth of perhaps 20 or 30 mm. Abrasion of other parts of the skull in general seemed not to affect their shape enough to cause difficulty in appreciating what characters might be taxonomic. The upper and lower surfaces of the beak were noted to be particularly free of abrasion, hence McCann's (1962c, p. 99, footnote) assumption that the extremely shallow depth of beak of the type of *pacificus* resulted from erosion is wrong. My measurement of beak depth at its midlength of 58 mm., furthermore, confirms Longman's (1926, p. 272) of 60 mm.

McCann (1961) had earlier studied a fragmentary specimen of a beaked whale consisting of the extremity of a beak and mandible with both teeth, and published convincing evidence that it represented an adult female *Hyperoodon planifrons.* He found that the beak of that specimen at a point 250 mm. from its apex was (McCann, 1961, p. 27) 103 mm. deep but only 78 mm. wide at the same place. The type specimen of *M. pacificus,* which McCann (1962c, p. 99) concludes is the skull of a female *Hyperoodon planifrons,* has a beak only 51 mm. deep and 80 mm. wide at a point 250 mm. from the apex of beak. The beak width is thus 0.76 of beak depth in the former and

1.57 in the latter. This is much too great a difference to attribute to two adult female beaked whales of the same species.

After having studied the apical alveoli of female specimens of *M. mirus* in American museums and those of the male *mirus* specimens in the British Museum (Natural History) and South African Museum, I recognized the apical alveoli of the type of *M. pacificus* as those of a male. They are more oriented upward than forward and have a more complete and firm edge to the alveolus such as might provide better support for a tooth that will project above the gum (a characteristic of males in most species of *Mesoplodon* and in *Hyperoodon planifrons* as well). Further evidence that the type of *M. pacificus* is not a female of *Hyperoodon planifrons* is that in *pacificus* the greatest depths of the right and left alveoli are, respectively, only 26.4 and 26.5 mm. and that teeth of the length of the adult female *Hyperoodon planifrons* recorded by McCann (1961, p. 25) as 58 to 67 mm., would have to project so far above these shallow alveoli as to erupt like teeth of a male.

For these above reasons as well as because of others implicit in the diagnoses provided for the genera *Hyperoodon* and *Mesoplodon* in the present paper, McCann's (1962c) suggestion that the type of *Mesoplodon pacificus* represents a female of *Hyperoodon planifrons* must be rejected. On the greater evidence available to me as well as more logical evaluation of the evidence available to McCann (1962c), the type of *Mesoplodon pacificus* is almost certainly not female and quite certainly not *Hyperoodon planifrons* (see also p. 254).

RELATIONSHIPS AMONG THE GENERA

Number and Position of the Teeth

It is generally accepted (Fraser, 1949, pp. 272, 275, 276) that in certain living genera of beaked whales only one pair of teeth reaches that fullness of development which is appropriate to its particular species and sex. These are *Hyperoodon*, *Ziphius*, and *Mesoplodon*. It is also generally accepted (Fraser, 1949, pp. 273 and 282) that another living genus of beaked whales has two pairs of teeth that reach the fullness of development appropriate to it, and that still another has about 48 pairs. These are, respectively, *Berardius* and *Tasmacetus*. After examining the above-listed materials, paying some particular attention to the teeth of *Mesoplodon*, but also those of other genera when these were easily available, I have observed no need for modification of these theses. It may be instructive to consider here some of the implications that not only number but the placement of these teeth have for the relationships among these living genera.

The development of only one pair of teeth in each of the species of *Ziphius*, *Hyperoodon*, and *Mesoplodon*, but two pairs in *Berardius* and about 48 pairs in *Tasmacetus* does in itself suggest the first three to be derivative genera, *Berardius* intermediate, and *Tasmacetus* primitive at least in this character. Even though so different in being so many, the functional teeth of *Tasmacetus* reveal in other ways its relationship to the other living genera of beaked whales: 1) The apical location of one pair of mandibular teeth which are of discretely greater size than its own other teeth suggests relationship especially to *Berardius* and, less closely, to *Ziphius*, *Hyperoodon*, and three of the species of *Mesoplodon*. 2) The occurrence of a diastema of 25 to 45 mm. (sample of three) between the large apical pair of teeth and the row of lesser mandibular teeth (fig. 2) suggests close relationships to *Berardius*.

Kirino's (1956) report that one individual in a sample of 65 specimens of *Berardius bairdi* had six mandibular teeth and a second individual had nine, suggests closer relationship of *Berardius* to *Tasmacetus* than to other living genera of beaked whales. The specimens of *Berardius bairdi* with nine teeth and another with five are illustrated

FIG. 2. Apex of lower jaw of *Tasmacetus* showing diastema between large apical alveolus and row of smaller closely set alveoli.

by Kirino (1956, pl. I), and reveal how these resemble *Tasmacetus* not only in having a large apical pair of teeth and a diastema posterior to it, but also in that on each ramus of the mandible the remaining smaller teeth stand in a close-set row posterior to the diastema. All of the supernumerary teeth that Kirino reported in *Berardius* occurred posterior to the diastema and the second pair of teeth. This suggests that the long spaces between the first and second normal pairs of teeth in *Berardius* are homologous to the diastema in *Tasmacetus,* and are evidence of their close relationship.

In *Ziphius* and *Hyperoodon* and *Mesoplodon* each adult develops only a single pair of teeth, set in conspicuous alveoli, and in all *Ziphius* and *Hyperoodon,* but only in three of the species of *Mesoplodon* this pair is located at the apex of the mandible just as is the large pair of teeth in *Tasmacetus* and *Berardius.* In the other nine of the 12 species of *Mesoplodon* the alveoli of the single pair of well-developed teeth are set back from the apex of the mandible a distance not less than 45 mm. (sample of 135 representing all 12 species), and in some individuals of the five species, *bidens, densirostris, layardi, grayi,* and *ginkgodens,* the distance exceeds 240 mm. In all of the other living genera the only well-developed pair of teeth (*Hyperoodon, Ziphius*) or the best-developed pair of teeth (*Berardius, Tasmacetus*), are apical in the mandible. Consequently, there is here an

FIG. 3. Tooth of *Mesoplodon grayi*, ad. ♂, ZM no. 1, showing symmetry of tooth and how deeply it stands buried in the alveolus; apex-to-root length of tooth 83 mm.

evolutionary departure from a condition otherwise characteristic of the living members of the beaked whale family, broadly expressed in the genus *Mesoplodon* (which nevertheless does have three species showing no departure): one showing only a little (*europaeus*, 70 to 100 mm.), three showing discretely more but intermediate amounts of departure (*stejnegeri, bowdoini, carlhubbsi*, 120 to 220 mm.), and the five others mentioned above which include three that approach the probable extreme for the genus of about 300 mm. (*bidens, densirostris*, and *layardi*). This development appears, of course, to be derivative; whereas apical location of the teeth within the genus *Mesoplodon*, exemplified by *hectori, mirus*, and *pacificus*, would be, within the genus, primitive.

The species of *Mesoplodon* in which the pair of well-developed teeth of the adult male is the most anteriorly inclined is *M. mirus* (see Harmer, 1924, pl. 4, fig. 9).

In four species of *Mesoplodon* the teeth of adult males are squared off at the bottom as if they stand upright in life. Cleaned teeth of these species placed in the alveoli of the mascerated mandibles sometimes show a slight anterior inclination of the long axis. These four species are: *europaeus* (Moore, 1960, figs. 2, 4), *grayi* (fig. 3), *ginkgodens* (Nishiwaki and Kamiya, 1958, pls. 5, 10), and *carlhubbsi* (Moore, 1963b, figs. 8, 15). In all of these four the teeth stand at intermediate distances from the apex of the jaw.[1]

Four more species have adult male teeth in which the anterior portion of the root is longer than the posterior, and which stand in the jaw with the long axis inclined posteriorly. Two of them are mildly inclined, *stejnegeri* and *bowdoini* (Moore, 1963b, figs. 8, 9, 12; Glauert, 1947, pl. 6) and two are strongly inclined, *bidens* (Fraser, 1946, fig. 11) and *layardi*. The mildly tilted ones occur at intermediate distances from the apex, the two more severely inclined posteriorly are among the three species with teeth most distant from the mandibular apex.

In the one other species of *Mesoplodon* in which the teeth are most distant from the apex of the mandible, *densirostris*, the long axis of the tooth is shown by Raven (1942, p. 37) and Moore (1958, fig. 4) to be inclined *anteriorly*. This provides an exception to the curious relationship that distance from the apex otherwise appears to bear to inclination of the tooth in this genus.

The geographic distribution of the above categories of tooth inclination and alveolar distance from apex falls into an interesting pattern in the genus *Mesoplodon*. Of those species with anteriorly inclined, apical teeth, *Mesoplodon hectori* is known only from the southern hemisphere, and *M. mirus*, on the distribution of 13 of the 14 of its known occurrences, is thought to be a primarily North Atlantic species (Moore, 1966, p. 54), although there is at least a stray recently reported from the South African coast (Talbot, 1960). *M. pacificus* is known from only one locality. That locality is in the southern hemisphere, but within the southern part of the tropics so that it may well be a stray from that core region of the tropical marine fauna called the Indo-Pacific Region, and a member of that fauna (see Davies, 1963, map, discussion p. 108). Geographically, *M. hectori* differs from *pacificus* in that its three known occurrences are all in the much cooler seas near New Zealand and the Falkland Islands, respectively about 40° and 50° south latitude.

In the category of *Mesoplodon* species with upright teeth and intermediate distance of teeth from apex of mandible, *grayi* in the tem-

[1] But an adult male specimen of *carlhubbsi* whose teeth look less mature at the root (Nishiwaki and Kamiya, 1959, fig. 10) than those of the La Jolla (type) specimen, is illustrated with the teeth mildly inclined (*op. cit.*, pl. 1, fig. 2, pl. 3, top and bottom) posteriorly, and perhaps quite correctly so, which suggests that *carlhubbsi* is intermediate between this group and the next.

FIG. 3a. Left side of audible of *Mesoplodon grayi*, ad. ♂, ZM No. 1, teeth in place.

perate waters of the southern hemisphere may replace *ginkgodens* and *carlhubbsi* of the North Pacific and *europaeus* of the North Atlantic. In the category of species with mildly backward-inclined teeth and intermediate alveolar distance from apex of mandible, *bowdoini* in the temperate waters of the South Pacific and Indian oceans might be thought to replace *stejnegeri* of very northern Pacific waters. Then, in the category of species with teeth that are strongly inclined backward and greatest distance from the apex of the mandible, there is *bidens* in the very northern North Atlantic, and *layardi* in the temperate waters of the Southern Hemisphere. As *M. densirostris* does not fit properly the combined categories of inclination of tooth and its distance from apex of the mandible, so also does it not fit the regional categories, but again must be classified by itself. It occurs in the tropics in the Indian Ocean at least, on both sides of the tropics in the Pacific Ocean, and is well known from the western side of the North Atlantic Ocean but unknown from the continental shelf of the eastern side (see Moore, 1966, p. 50, for postulates on this distribution).

Implications for Relationships

Kellogg (1928, p. 61) after reviewing the fossil hyperoodontoids, concluded that, "The paleontological evidence bearing on the ancestry of the [hyperoodontoids] indicates that they were derived from ancestors with [numerous] functional teeth in both jaws." Since number of teeth has thus evidently tended strongly to diminish in the history of this family, possession by *Tasmacetus* of teeth in both jaws totaling about 48 pairs may be regarded, when other evidence is equivocal, as indicating the most primitive of the living genera. Retention of two pairs by *Berardius* suggests it is more primitive than all three of the remaining genera living today, each of which has but a single pair. The existence of a notable diastema behind the apical mandibular teeth also suggests close relationship between *Tasmacetus* and *Berardius*. Progressive retreat of the single pair of mandibular teeth from the apex of the mandible, and corresponding change of the orientation of the tooth from anterior inclination through vertical posture to strong posterior inclination suggests a further possible arrangement of the species of *Mesoplodon* on a primitive to derivative scale. This would be *hectori, mirus, pacificus, densirostris, europaeus, carlhubbsi, ginkgodens, grayi, bowdoini, stejnegeri, bidens,* and *layardi*. Because of these derivative extremes of tooth position in *Mesoplodon,* this genus would qualify as the most derivative of the genera in this set of characteristics. A linear arrangement of the genera on the characteristics of number and position of teeth should therefore be: *Tasmacetus, Berardius, Ziphius, Hyperoodon,* and *Mesoplodon.*

SIZE AND SHAPE OF TEETH

Tasmacetus

The shapes of the teeth of *Tasmacetus* are illustrated by Oliver (1937, pl. 4, fig. 10). These are somewhat conical, but have an enlarged base which varyingly produces an asymmetrical pear shape. Thus, the lateral profiles of a *Tasmacetus* tooth are convex proximally, concave and then distally straight. Sizes of the large pair of apical mandibular teeth (Oliver, 1937, p. 377) are, left and right, respectively: greatest length 42 and 41 mm., greatest antero-posterior diameter 23 and 24 mm., greatest transverse diameter both 16 mm. (In personally measuring the longer of these two teeth, I obtained 42, 23, and 17 mm., respectively, and estimated one mm. of length to have been lost from wear. At the University of Canterbury some of the teeth of *Tasmacetus* were seen but not made readily available for measuring or photographing.)

Hyperoodon

Much information is available on supernumerary teeth in *Hyperoodon ampullatus* (Thompson, 1846; Turner, 1885; Boschma, 1950;

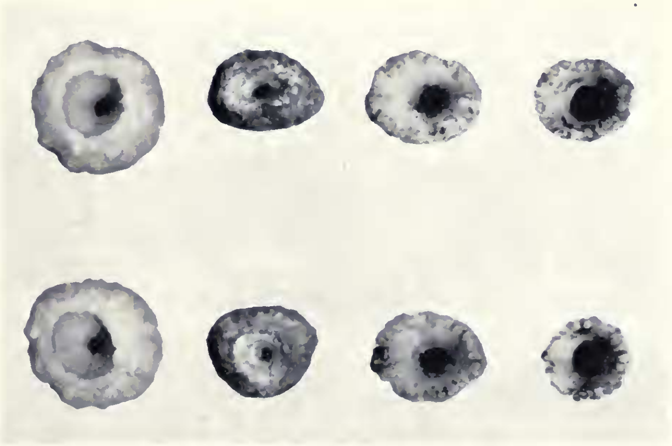

FIG. 4. Root ends of four pairs of teeth of *Hyperoodon ampullatus* showing pulp cavities; specimens of British Museum (Natural History) and all from British Isles.

TABLE I.—Sexual dimorphism in ratio of greatest length to greatest width of teeth of *Ziphius* and *Hyperoodon*

Ziphius cavirostris

Adult Males			Adult Females		
tooth	tooth	authority	tooth	tooth	authority
0.65	....	Moore (1953, p. 150)	0.214	0.202	Fraser (1942, p. 24)
0.618	0.636	Fraser (1942, p. 27)	0.232	.....	True (1910, p. 55)
0.555	0.58	Fraser (1942, p. 26)	0.25	0.254	new
0.476	0.528	new	0.304	0.289	Paulus (1962, p. 26)
0.46	.....	True (1910, p. 55)	0.246	0.25	new
0.52	.....	True (1910, p. 55)	0.254	.....	Kenyon (1961, p. 73, pl. 1)
0.52	.....	True (1910, p. 55)	0.340	.....	Haast (1877, p. 432)
0.704	0.666	Harmer (1927, p. 49, fig. 21a)	0.307	.....	Cabot (1965, p. 72)
0.618	0.583	Fraser (1934, p. 31, fig. 7)	0.214	.....	Haast (1877, p. 441)
			0.233	0.230	Haast (1880, p. 243)
			0.277	0.264	Stephen (1931) corrected identification

Hyperoodon planifrons

Adult Male			Adult Female		
right	left	authority	tooth	tooth	authority
0.627	0.632	Hale (1931, p. 298)	0.293	0.310	McCann (1961, p. 25)

TABLE I.—Sexual dimorphism in ratio of greatest length to greatest width of teeth of *Ziphius* and *Hyperoodon*—*Continued.*

Hyperoodon ampullatus

Tooth				Tooth				
greatest length	greatest width	ratio	depth pulp cavity	greatest length	greatest width	ratio	depth pulp cavity	length of body
				Adult Males				
40.05	20.2	0.505	..	....	....	.....	..	.... BM 1889.11.6.1 (=1378E)
33.1+3	13.0	0.360	0	34.4+2	14.7	0.404	0	28 ft. RSM Huxter, Shetland, 27 Aug. 1932
				Immatures of Somewhat Uncertain Sex				
40.6	15.7	0.390	23	40.3	15.5	0.390	19	.... BM 1378c
41.1	18.7	0.445	25	....	....	.....	..	25 ft. BM 1846.12.13.40
43.1	18.3	0.424	13	44.2	19.6	0.444	12	25 ft. BM, SW–1917–25
36.8	14.5	0.405	7.5	33.9+3	14.5	0.393	7	23½ ft. BM, SW–1927–27
37.2	13.0	0.350	24	37.4	11.6	0.310	25	21 ft. BM, SW–1938–25
39.9	14.3	0.358	24	40.5	14.1	0.310	25	.... RSM 1936–76
38.1	17.0	0.446	27	37.6+1	18.2	0.472	27	.... RSM, S. Queensbury, 20 July '51
40.7	15.4	0.379	23	....	....	.....	..	.... RSM 1938–63
28.4	8.2	0.288	27	26.2	8.7	0.332	22	17 ft. RSM, Prestonpans, 12 Aug. 1932

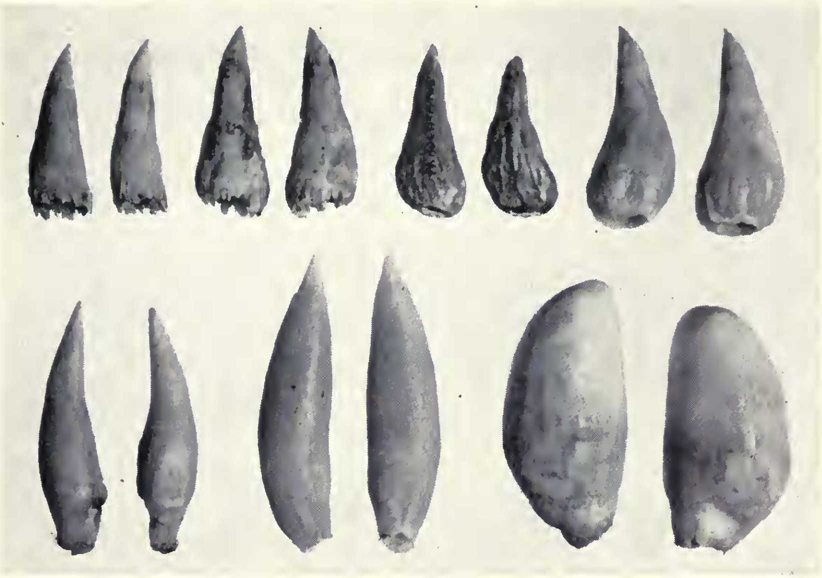

FIG. 5. Upper: pairs of teeth of four individuals of *Hyperoodon ampullatus*; the two pairs at left are immatures; those at right approach adulthood; all British Museum (Natural History) specimens from the British Isles, courtesy Miss J. E. King.

Lower: pairs of teeth of three individuals of *Ziphius cavirostris*; all from La Parguera, Puerto Rico, courtesy of Donald S. Erdman; the middle pair is of ad. ♀, FMNH 95286; the left pair is ad. ♀ and the right pair is ad. ♂, both lent from a private collection. Upper and lower in a single photograph, hence same scale.

Fraser, 1953), the northern bottle-nosed whale which, because it occurs in European waters, is in many ways better known than the other living species, *H. planifrons.* So little is known about the normal teeth of *Hyperoodon ampullatus* that it seems of value here to illustrate the normal teeth of several specimens of varying development. In Figure 4 the state of closure of the pulp cavities in these is revealed. The ones with the most open and deepest pulp cavities, presumably in a general way the youngest, are noted to have finger-like projections forming the rim around the pulp cavity which are, as far as I am aware, unique among the teeth of immature beaked whales, and may prove of value in distinguishing between teeth from immatures of *H. ampullatus* and those of *Ziphius* at least. In Table 1 closure of the mouth of the pulp cavity may be observed to progress with increase in body length of the animals, increase in dimensions of the teeth, and decrease in depth of the pulp cavity.

The shape of *Hyperoodon* teeth, described above as primitive, is shown in Figure 5 in contrast with teeth of three adult specimens of *Ziphius cavirostris* (left to right—♀ ♀ ♂), all from Puerto Rico. Donald S. Erdman (1962) provided the larger pair of female teeth, together with the skeleton, from a 1961 stranding at La Parguera, P. R. (FMNH 95286), and Mr. Erdman lent the two other pairs from individuals in a stranding said by acquaintances of Erdman's to have involved four small whales at La Parguera, P. R., on or shortly before December 9, 1965.

Adult Males of *ampullatus.*—Fraser (1949, p. 272) gives a description of a pair of teeth taken from a 26-foot male, but I have found no publication of a first-hand description or illustration of the teeth of a male more definitely known to be fully adult, and identified as this species. Nor in examining 67 items in the scientific literature dealing with this species have I found clear reference to such a description or illustration. The teeth that have been reported upon by scientists are almost exclusively of female or young specimens, which have stranded or been captured in coastal waters. Adult males are said to be seen far at sea where they have been sought at times by small commercial whaling vessels on which hazards of life and limb have been regarded so discouraging for whaling men as to be perhaps prohibitive for a scientist.

To help me in this effort to evaluate relationships among the living genera of beaked whales, Dr. F. C. Fraser has generously measured and sketched the tooth and alveolus of the skull of a fully adult male (BM 1889.11.6.1=1378 E) exhibited in the British Museum. Figure 6 shows the right tooth *in situ* on the apex of the right ramus of the mandible, and its measurements are shown in Table 1. It was evidently exposed in life, for the crown is worn off in an oblique plane tilted downward on the right. It is apparent from this and the teeth from young specimens of varying proximity to maturity, from the British Museum and lent by Miss J. E. King (see fig. 5), that the teeth of adult *Hyperoodon ampullatus* are characterized by a slight but definite bulbousness at the proximal end. This results in shape rather like a pear in that the profile of each whole tooth is convex near the proximal end but becomes slightly concave toward the apex. In this it differs from all living species of other genera of beaked whales (whose teeth are known) excepting *Tasmacetus shepherdi* (Oliver, 1937, pl. 4, fig. 10). This similarity and the very small proportional size of these apical mandibular teeth suggest that the teeth of *Hyperoodon ampullatus* have not in fact developed or differentiated

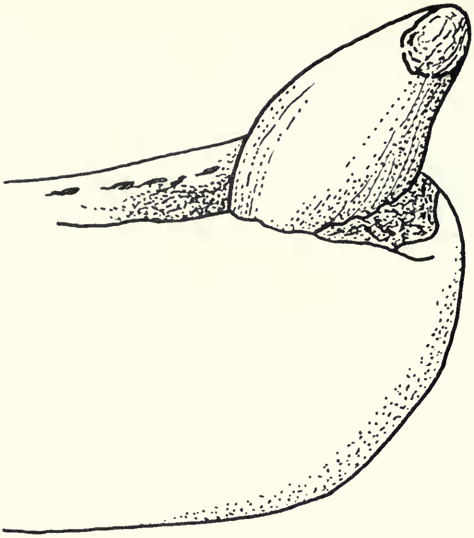

FIG. 6. Lateral view of right tooth of ad. ♂ *Hyperoodon ampullatus*, BM 1889. 11.6.1. From original sketch by F. C. Fraser.

more than the corresponding apical teeth of *Tasmacetus*, and therefore while more vestigial and derivative in number, they are as primitive in development.

In a loan of teeth from seven beaked whales (five *Hyperoodon ampullatus* and two *Ziphius*) received from Dr. Arthur S. Clarke of the Royal Scottish Museum is the only pair of apical teeth of *Hyperoodon ampullatus* observed by me to have the pulp cavities entirely filled at the root. This pair of teeth comes from an individual stranded on reefs a mile east of Huxter, Sandness, Shetland, 27 August 1932, and said to have "measured 28 feet in length." Dimensions of this pair of teeth are provided in Table 1. Stephen (1932, p. 164, fig. 2) misidentified the Huxter whale as an old female *Ziphius cavirostris*, and we offer photographs of its teeth (fig. 7) to supplement his and to show more adequately their important character. The identification becomes easier, of course, when one has for comparison even such a small series of teeth from both *Ziphius* and *Hyperoodon* as offered here in Figure 5. In study of photographs of the teeth of adult females of *Ziphius*, I observe that the greatest diameter

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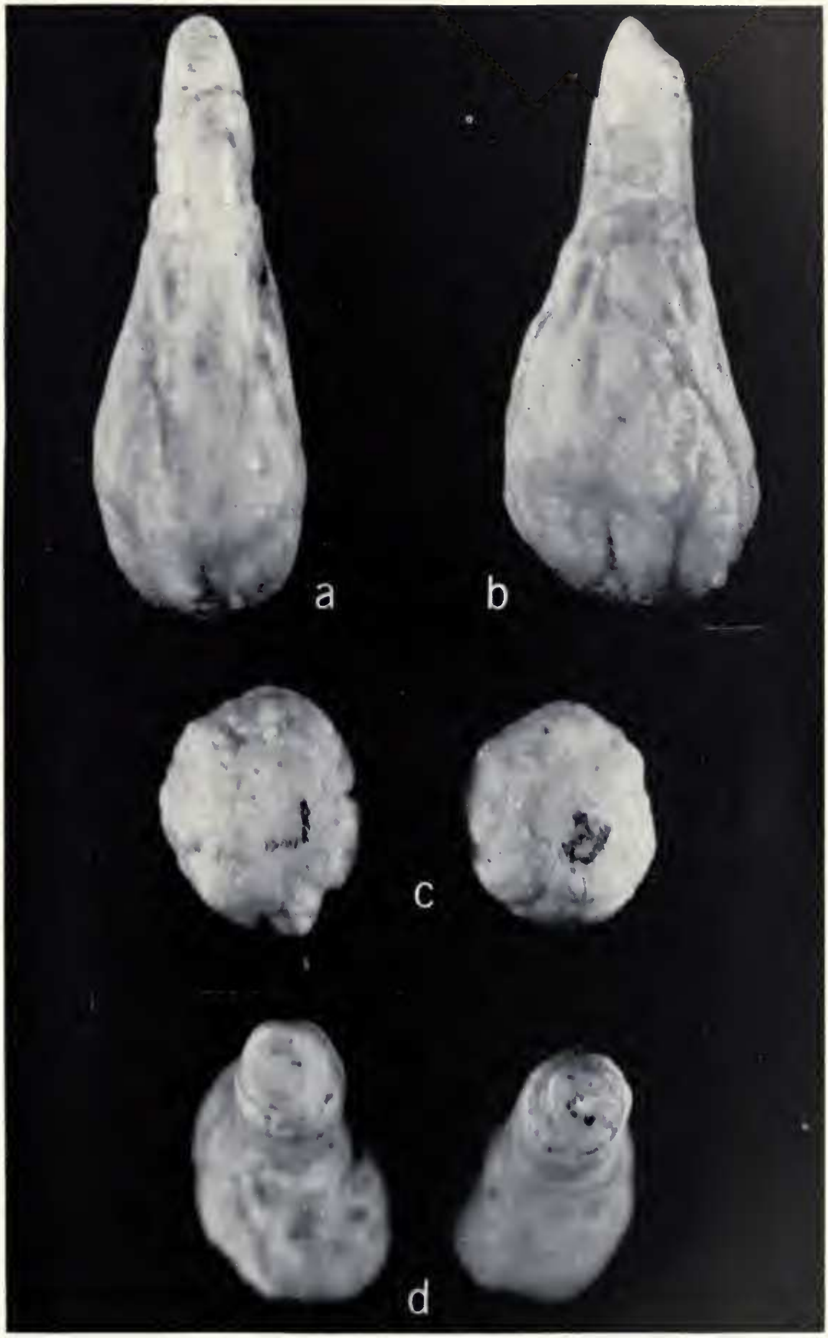
FIG. 7. Teeth of adult male *Hyperoodon ampullatus* from Huxter, Sandness, Shetland Ils. showing: the posterodorsal view (a), with scourings attributed to agonized biting of gravel, and apical wear facet; left lateral view (b) of same (left) tooth; basal ends (c) of both teeth, pulp cavities filled; apical view (d) with wear facets on both teeth enlarged.


a
b
c
d

seems characteristically to occur nearer to 0.40 than to 0.25 of the tooth's length from the basal end. The teeth of adults of *Hyperoodon ampullatus,* including the Huxter whale's, are bulbous at the root, and pear-shaped so that their greatest diameter appears to come nearer to 0.25 of the tooth's length from the proximal end. The stated 28-foot length of the Huxter whale still greatly exceeds published lengths for *Ziphius* that were made with obvious care by a zoologist, and it far exceeds the length measurements since provided by Omura, Fujino, and Kimura (1955, p. 117) for 85 individuals of *Ziphius* from Japanese waters, only one of which had reached 23 feet.

Stephen (1932, p. 166) referred to the Huxter whale's sex as "undoubtedly female," but offered no evidence for this. The apices of both teeth are crudely cut as if by accidental contact with sharp, very hard, rough material, but I have seen teeth of a newly stranded adult male *Ziphius* so freshly and crudely scored that it seemed certainly done on rocks while dying in shallow water. When the teeth of the Huxter specimen are juxtaposed and oriented correctly, it is seen that the scoring (some of which extends to the midlength of each tooth) is limited to their upper surfaces (fig. 7a) and may also have been acquired in the death struggle, for example from biting gravel of small sharp stones. Under magnification it becomes apparent that at the apices of the teeth these scourings are superimposed upon preexisting flat, wear surfaces which were relatively smooth and which truncate the apices of the teeth (fig. 7b and d) on a plane probably congruent with that of the surface of the gum. On the left tooth this wear surface is 3.5 × 5 mm. On both teeth it is confined to the portion of the tooth capped by dentine. In view of this evidence of eruption of the teeth in maturity, the 28-foot body length attributed to the animal (Fraser, 1949, p. 270, says that, "males [attain] to a length of some 30 feet and females to about 24 feet."), the evidence from *Hyperoodon planifrons* that an adult male's teeth erupt but that an adult female's teeth do not, the present investigator recognizes the Huxter specimen as an adult male. One might object that the small size of this apical pair of teeth mitigates against its being male, but my (fig. 10) records of a large sample of teeth from another species of beaked whale, *Mesoplodon bidens,* lead me to expect greater variation in size of apical teeth in male *Hyperoodon ampullatus* than would be inferred by this sample of two.

Species *planifrons.*—The teeth of the species *Hyperoodon planifrons* are beginning to be better known from the excellent figures and measurements by Hale (1931) of an adult male; the fine photograph of the tooth of the adult female from New Zealand (McCann, 1961, pl. 3); the drawings, measurements, and terse but judicious description by Fraser (1945, pp. 26, 27) of an immature female from South Georgia; and now a good photograph with rather too few measurements, but some helpful comment from Miss Tietz (1966, p. 106) of an immature male from South Africa. Miss Tietz calls her South African specimen an adult but notes that the teeth were definitely not erupted, that the pulp cavity of the tooth was open at the base, and that the tooth and skull measurements of her specimen showed it to be near the size of the immature female reported by Fraser. Miss Tietz acknowledges these to be characters of youthfulness, but remains enigmatic as to why one should call the South African specimen adult. The illustrations of the immature female from South Georgia (Fraser, 1945, pp. 28, 29) show the epiphyseal sutures of the thoracic, lumbar, and caudal vertebrae to be open. By this and the the similarities of other ontogenetic characteristics noted, it seems safe to say that the South African *H. planifrons* is morphologically immature. Since Fraser's (1945, p. 22) table of skull measurements shows the sizes of the specimens in the La Plata Museum, Argentina (Moreno, 1895), to be smaller in most measurements than the immature female from South Georgia, we still know of but two adults, the South Australian male and the fragmentary New Zealand female.

Another fragmental specimen consisting of 115 mm. of the mandible with two terminal teeth, of another female beaked whale, was illustrated and measured, and thought possibly of *Hyperoodon planifrons* by Waite (1913), and affirmed strongly by McCann (1961, p. 24). McCann said the specimen is no longer available, and formed his opinion from Waite's publication. The tooth of the specimen in question as illustrated whole (Waite, 1913, pl. VIII, fig. 2), more nearly resembles the shape characteristic of teeth of adult females of *Ziphius cavirostris* illustrated by True (1910, pl. 38, figs, 3, 4), Fraser (1942, pl. II, fig. c), Kenyon (1961, pl. I, left), and Moore (1963a, p. 3), than it resembles the illustrated tooth of the one specimen now acceptable as an adult female of *Hyperoodon planifrons* (McCann, 1961, pl. 3).

The observed differences between teeth of adult females of *Ziphius cavirostris* and this one tooth of an adult female of *Hyperoodon planifrons* are: 1) The greatest diameter of a tooth of *Ziphius* occurs nearer a point 0.40 of tooth length from the basal end, but in *Hyperoodon planifrons* it occurs at a point nearer to 0.25 of the length. 2) The profile of any part of the surface of the apical half of the tooth of *Ziphius* is convex, but in the apical half of the tooth of *H. planifrons* a slight constriction in the circumference of the tooth creates a slight concavity in either profile (McCann, 1961, pl. 3). 3) In *Ziphius cavirostris,* in which the apical cone of dentine has not been resorbed, the profile of the tooth continues proximally from it smoothly, but in the one known adult female of *Hyperoodon planifrons* a sudden enlargement of the diameter immediately below the dentine makes an abrupt step in the profile. The first two of these above-described characters of the tooth of the one adult female of *Hyperoodon planifrons* fit the teeth of the examples of *Hyperoodon ampullatus* illustrated here (fig. 5).

In *Hyperoodon planifrons* the known samples of teeth of the one adult male diverge more from the one adult female in the ratio of greatest width to greatest length (0.632 and 0.627 compared to 0.310 and 0.293) than is average for the samples of *Ziphius.* While too little seems to be known about teeth of adults of *Hyperoodon ampullatus* to permit determination of the presence of sexual dimorphism, the evidence is strong that the southern hemisphere species of *Hyperoodon* has achieved striking sexual dimorphism in shape of teeth.

Ziphius

In the goose-beaked whale the teeth of the adult males are found by the evidence assembled in Table 1, to be distinguished from adult females by the ratio of length to width of teeth. Twelve teeth of eight adult males have greatest width more than 0.40 (0.460 to 0.704) of greatest length; whereas 15 teeth of ten adult females have greatest width less than 0.40 (0.340 down to 0.202) of greatest length of tooth. Thus we find relatively strong evidence that sexual dimorphism in size and shape of teeth frequently reported in the genus *Ziphius* is consistent, and offer a definition of it (see fig. 5).

Related to the differences in shape and contributing to them is the characteristic that in adults of *Ziphius cavirostris* (and *Hyperoodon planifrons*) the male teeth erupt and wear but the female teeth remain unerupted or cryptic below the gum. No doubt rare exceptions to this may eventually be found and convincingly reported, but in much survey of the *Ziphius* literature no such certain exception has turned up. For an example of what one may encounter as unconvincing exceptions, Haast (1880, p. 242) reports a "young female" 19½ feet long of *Ziphius cavirostris* which he personally examined freshly stranded and found the two apical teeth, conical and sharply pointed, to project one-half inch above the gum. However,

FIG. 8. To facilitate future distinction of ad. ♀ *Ziphius cavirostris* from adult ♀ *Mesoplodon mirus*, one pair of each (respectively USNM 312888 and USNM 175019) are shown together: dorsal view (a), lateral view (b), all teeth same scale.

his table of measurements shows the genital opening to be 35 cm. from the anus, which, if correct, is convincing evidence that its sex is male. The teeth were an inch in diameter where emerging from the gum, but the thickest tooth of a female of this species (Haast, 1877, p. 432) in Table 1 is only 18.3 mm., and the slenderest for a male is 25 mm. (Fraser, 1942, p. 26; True, 1910, p. 55).

The dimensions of the teeth of a beaked whale specimen that stranded in January 1931 at Geirnish, South Uist, Scotland, now registered as specimen no. 1931.27 at the Royal Scottish Museum, are given in Table 1. As mentioned in the first paragraph of this paper, this South Uist specimen was misidentified and published as *Mesoplodon mirus* by Stephen (1931). In October 1963 Dr. Arthur S. Clarke showed me the skull of this specimen, and I saw at once that the nasal bones and premaxillaries possessed the characteristics of *Ziphius*. (See item no. 2 in the "Diagnosis of *Ziphius*" and item 1a in the "Key to the Genera by Characters of the Skull.") Subsequently, Dr. Clark lent me the teeth of this South Uist specimen, which are, as shown in Figure 1, unusually compressed for teeth of *Ziphius*, but comparison of the relative amount of this compression reveals further evidence, if any were needed, that this specimen is no *Mesoplodon* but *Ziphius cavirostris*. The greatest transverse diameter of the tooth (i.e., perpendicular to its long axis), divided by the greatest transverse diameter perpendicular to the first such diameter are, respectively: right tooth, 14.5 ÷ 10.2 mm. = 1.42; left tooth, 14.1 ÷ 10.1 mm. = 1.395. As shown below in the "Key to the Living Genera by Characters of the Teeth," these ratios distinguish the South Uist specimen from the living species of the genus *Mesoplodon*, whose adult teeth are known, and place it in the genus *Ziphius* (see fig. 8).

Berardius

The North Pacific species of the four-toothed whales is the largest of the living species of the Hyperoodontidae, and differs from its closest rival for this distinction, the North Atlantic species of *Hyperoodon*, by producing an apical pair of teeth at least somewhat more proportionate to the size of the whole animal. This apical pair of teeth of both species of *Berardius* resembles the teeth of all of the species of *Mesoplodon* in being laterally compressed. If this similarity results from a single origin of such compression, a great deal of other evolution has taken place since that fork in the lineage.

It seems worthwhile to digress from relationships here to say how the compressed teeth of *Berardius* may be distinguished from those of *Mesoplodon*. The greatest transverse diameter of an apical tooth of *Berardius* exceeds 28 mm. (30–62) in the available sample of six and this distinguishes these teeth of *Berardius* from those of all living species of *Mesoplodon,*[1] except adult males of *M. densirostris*. Apical teeth of *Berardius* may easily be distinguished from teeth of adult male *M. densirostris,* however, by their greatest antero-posterior width divided by greatest length of tooth from apex to most distant point on root (close to the long axis of the tooth). In 11 *Berardius* this is greater than 0.70 (0.80–1.10) but in seven male *M. densirostris* it is less than 0.70 (0.44–0.62).

Mesoplodon

All of the 12 living species of this genus, whose teeth are known, develop their single pair of mandibular teeth so laterally compressed that this one character distinguishes *Mesoplodon* from all the other genera excepting *Berardius*. One finds in study of this genus, however, that what is known about size and shape of the teeth is complex because of the pronounced differences between the teeth of many of the living species, and because of the sexual dimorphism that has been demonstrated in the teeth of some species. Valuable detail could be contributed here to knowledge of the nature and extent of sexual dimorphism, ontogenetic change, and individual variation of some of the dozen species of *Mesoplodon,* but those extensive details would be better treated in a revision of that genus. Here I shall limit consideration to those characters of the teeth which seem to have taxonomic value at the generic level, or to indicate something about the evolutionary relationship of *Mesoplodon* to the other living genera.

The characteristic flattening of the teeth of *Mesoplodon* in, or toward, a vertical antero-posterior plane must be a derivative character if these compressed teeth have evolved from generalized, simple, odontocete teeth that are round in cross-section and possess a cone-like apex, as one might well presume from consideration of the teeth of *Tasmacetus*.

The teeth of *Mesoplodon* attain great length in the second largest species of the genus, *M. layardi*. The longest personally measured is 330 mm. In individuals of three other species the teeth may attain lengths greater than 150 mm.: *M. densirostris, M. stejnegeri,* and *M. carlhubbsi*; and *M. bowdoini* approaches that with a greatest length

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[1] For which the teeth of adult males are known. However, I predict that when the teeth of adult males of *hectori* and *pacificus* are known they will also be found to measure less than 28 mm.

of 148 mm. In greatest antero-posterior width, measured at approximately right angles to the long axis of the tooth, individuals may exceed 100 mm. in one species, *M. ginkgodens*; may surpass 90 mm. in two other species, *stejnegeri* and *carlhubbsi*; and may exceed 80 mm. in three more species, *densirostris, grayi,* and *bowdoini.* These dimensions far surpass those of teeth of *Ziphius* and *Hyperoodon* as shown in Table 1, even though some of these *Mesoplodon* species are much smaller animals. Males of one of the smallest species, for an extreme example, *densirostris,* measure only about 4.5 m. in length but may have teeth more massive than those of a 10-m. *Berardius bairdi.* The greatest length, width, and thickness of the bulkier tooth of each is, respectively, 140, 87, and 49 mm. for *M. densirostris* compared to 92, 100, and 44 mm. for *B. bairdi.*

It is generally characteristic of *Mesoplodon* that in males the exposed portion of the tooth possesses a small, sharp apex of dentine which, in species with upright teeth, typically stands up from the top edge of the flattened tooth as a denticle, or a little tooth upon a tooth (e.g., fig. 9). On the unerupted tooth of the adult female this cusp or denticle is located in a manner somewhat corresponding to that on the erupted tooth of the male of its species. In both male and female of most species, the cusp leans laterad away from the long axis of the tooth. But it is the difference between species in the location of this denticle that corresponds to the above-described differences between species: 1) anterior or posterior inclination of the tooth, and 2) its distance from the apex of the mandible.

In that above-described category of species in which the tooth is apical and its long axis inclined anteriorly, we observe that in an adult female of *hectori*[1] the denticle is on the dorso-anterior edge of the tooth which, if the tooth stood with its long axis vertical, would be the posterior shoulder of the top edge of the tooth.

In the category of species in which the tooth stands at an intermediate distance from the mandibular apex and with its long axis nearly vertical, the denticle is located in the middle of the top edge where it is transected by the long axis of the tooth (*europaeus,* Moore, 1960, fig. 7; *ginkgodens,* present paper, fig. 9; and *grayi,* present paper, fig. 3) or is located between the midpoint of the top edge and the most anterior point on the top edge of the tooth (*carlhubbsi,* Moore, 1963b, fig. 8, center).

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[1] The skull and jaw of an adult female specimen of *hectori* have come to me on loan from the Tasmanian Museum in the latter days of completing this manuscript, through the courtesy of Dr. Eric R. Guiler who collected it (Guiler, 1967).

FIG. 9. Teeth of adult male *Mesoplodon ginkgodens*, BM 1957.4.5.1, illustrating distance of teeth from apex of mandible, and the denticle. Compare with Figure 3.

In the category of teeth of intermediate distance from mandibular apex and mildly inclined posterior of vertical, the denticle forms the apex at the top of the anterior edge of the tooth (*stejnegeri*, True, 1910, pl. 12; Moore, 1963b, fig. 9; *bowdoini*, Andrews, 1908, fig. 2; Oliver, 1922, pl. 2; and Moore, 1963b, fig. 12).

The last category of species with teeth located farthest back from the apex of the mandible and with their long axes inclined strongly posterior, must here be subdivided into two categories. One, *bidens*, is like the previous category to the extent that the denticle is at the top of the anterior edge of the tooth, but when not obscured by excessive wear, the denticle extends forward well past the line of the antero-dorsal edge of the tooth (fig. 10; and True, 1910, pl. 2, fig. 3). The second, *layardi*, has a denticle which differs so strikingly from all the other species of *Mesoplodon* in location, that together with the extraordinary length of the tooth it may justify a special subcategory for the strap-toothed whale. The denticle is not on the apex of the tooth, nor is it on the anterior or posterior edge; instead, it is on the outer side of the tooth rather near its apex (Owen, 1870, pl. 1, figs. 2, 5). The implications of this will be considered below.

There is one species of *Mesoplodon* in which the tooth of the adult male can hardly be said to have a denticle and which does not fit well into any of the above four categories of combined inclination-of-tooth-axis and alveolar-distance-from-mandibular-apex. This species is *densirostris*. The inclination of the axis of its tooth is rather strongly anterior (Raven, 1942, fig. 13; Moore, 1958, fig. 4) and its apex, where the denticle must be before it wears off, is near the anterior edge of the tooth. The position of the tooth of the adult male in this species is extraordinarily elevated above the level of the mandibular symphysis on a pulpit-like rise of the alveolis above the ramus supporting it.

Summary and Implications

The teeth of adult males of *Hyperoodon ampullatus* are illustrated possibly for the first time with correct identification. Comparative illustrations of teeth of morphologically immature specimens of this species, teeth of adults of both sexes of *Ziphius cavirostris*, teeth of the adult female of *Mesoplodon mirus*, and also a table of tooth dimensions of adults of *Hyperoodon* and *Ziphius*, are presented to facilitate future identification of stranded specimens of any of these three. Sexual dimorphism in the teeth of adult *Ziphius* is demonstrated in a larger sample than previously possible. Teeth of *Berardius* are distinguished by measurements from those of the species of *Mesoplodon*.

FIG. 10. Teeth of *Mesoplodon bidens*, presumed by evidence of natural wear, hence eruption, to be of adult males, all from British Isles, all British Museum (Natural History) specimens.

The structure of the teeth of all these genera, when compared with those of one of the earliest fossil Hyperoodontidae, *Diochoticus,* are probably derivative in the sense of having: 1) become simplified in form of tooth (*Tasmacetus, Hyperoodon, Ziphius*); 2) radiated intragenerically in tooth size and structure (*Mesoplodon*); 3) become compressed (*Berardius, Mesoplodon*); 4) radiated to produce many species modified variously as to location of the pointed tip on the front, middle or rear of the top edge of the tooth (*Mesoplodon*). These factors taken together suggest for the living genera a linear scale of most-primitive-to-most-derivative as follows: *Tasmacetus, Hyperoodon, Ziphius, Berardius, Mesoplodon.*

Within the genus *Mesoplodon* the inter-specific variation in location of the denticle on the body of the tooth is rather consistently associated with distance of tooth from the mandibular apex of the mandible and orientation of the tooth. By this set of three related variations the species may be linearly arranged on a most-primitive-to-most-derivative scale as follows: *hectori, mirus, pacificus, europaeus, ginkgodens, grayi, carlhubbsi, bowdoini, stejnegeri, bidens, layardi,* and not specifically at the end of this progression but apart from it, although otherwise one of the most derivative species because of the structural characteristics of the mandible of the male, is *densirostris.*

ALVEOLI

The alveoli of the teeth of *Tasmacetus* were described only as "shallow" by Oliver (1937, pp. 376, 377), but their pertinence to intergeneric relationships invites greater detail. Most alveoli of all the three specimens examined contained pads or platforms of delicate dendritic bone, rather similar in structure in some alveoli to the dendritic lichens commonly called reindeer moss. In other alveoli, the branches of these dendrites apparently have become more fused with those of others and the structure of the platforms is more sponge-like.

In the Dominion Museum specimen (no. 613), a mandible with which there were no teeth, the absence of these platforms from some alveoli led me to presume that the platforms represented a stage in the filling in of alveoli by bone where in life some teeth had been lost. The University of Canterbury Museum specimen (no. 1063), however, had all of its teeth present, and all of the alveoli contained these bony platforms; hence, absence of some of these delicate structures from alveoli in other specimens is better explained by their having been eroded away in handling as specimens, or in washing on the beach as bare bones.

These bony platforms or pads in the alveoli of the mandibular teeth usually fill the rather shallow alveoli almost to the brim and generally leave a little space between the periphery of the pad and the rim of the alveolus. In the alveoli of the maxillary teeth the platforms may rise out of and above the very shallow alveoli.

Thus, instead of teeth with a narrow root secured deep in a bony socket as in *Mesoplodon, Tasmacetus* has teeth with swollen, bulbous roots which sit upon platforms of dendritic or spongiform bone in very shallow alveoli. The apical, larger pair of teeth in *Berardius* have shallow alveoli with spongiform or grossly cancellous pads in their bottoms. These are proportionally deeper alveoli than those of *Tasmacetus,* but proportionally much less deep than those of *Mesoplodon.*

Nothing is yet known about female teeth in *Tasmacetus,* but sexual dimorphism, if any, present in the teeth of *Berardius* was not detected by Omura *et al.* (1955, table 4), nor demonstrated by Kirino (1956, p. 432), although the latter then thought it would be possible to show that "the teeth of the female are, statistically speaking, inferior to those of the male in all their dimensions." Be that as it may, the teeth of the female *Berardius* do erupt, wear away at the apex, and approximate (if not equal) the size of male teeth (Omura *et al.,* 1955, table 4). In view of the relative, if not complete, lack of sexual dimorphism in the teeth of *Berardius,* and the evidence of close relationships between *Berardius* and *Tasmacetus* presented here, it would now seem especially unwise to anticipate that strong sexual dimormorphism will be found in the teeth of *Tasmacetus.*

It may have become apparent from the above that comparisons of the alveoli of the mature, erupted teeth of *Tasmacetus* and *Berardius* need to be made with those of the adult *male* teeth (not female) in the other genera. In *Ziphius,* only teeth of adult males have been shown to erupt and wear; those of females do not (True, 1910, p. 57; Fraser, 1942, p. 29) erupt but remain cryptic in the alveolus beneath the gum. In the male of *Ziphius* as it grows older, ". . . passage from the cylindrical to the fusiform shape . . . is brought about . . . by an absorption of the tooth root, a wearing down of the [exposed apex], and a very great thickening of the [remainder of the tooth by] investing cement" (Fraser, 1942, p. 29, and pl. 2, c to h). On the pertinent matter of the alveolus, True (1910, p. 57) has noted, ". . . in adult males the teeth are almost entirely protruded from the alveoli, which are filled with a coarse bony network." That this is very similar, indeed, to the apical alveoli of *Tasmacetus* and *Berardius* is obvious, for example, in True (1910, pl. 23, fig. 1), where pads or platforms of dendritic or spongiform bone may be seen in a male *Ziphius*.

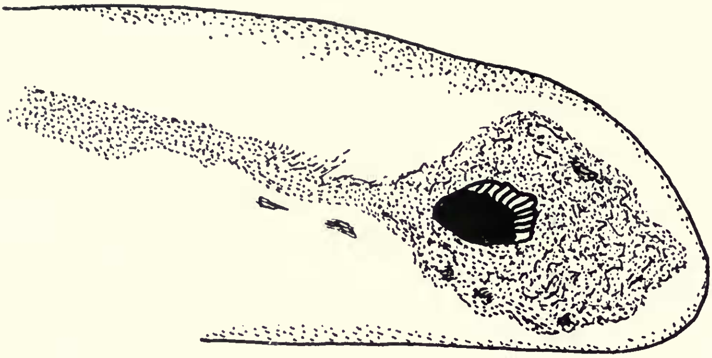

FIG. 11. Dorsal view of apex of left ramus of the mandible of an adult male *Hyperoodon ampullatus*, BM 1889.11.6.1, showing the alveolus. Compare description in text. From an original sketch by F. C. Fraser.

In *Hyperoodon* there is strong sexual dimorphism in the teeth of the southern species *planifrons.* The tooth of the one adult female known remains slender and unerupted (McCann, 1961, pl. 1, fig. 8), but that of the one adult male known erupts, wears (most peculiarly), and grows stout (Hale, 1931, fig. 11). Comparison with photographs of these same male teeth in place (Hale, 1931, figs. 9, 10) reveals that at least half of their length (57 and 59 mm.) protrudes above the bone of the alveolus. The implicit alveolar depth of only about 30 mm. suggests that the alveolus in the adult male of this species must also be filled in with bone, as noted above in *Ziphius.*

No published observations describing or illustations depicting the alveolus in adult males of *Hyperoodon ampullatus* have come to my attention, and here, as in the case of the tooth of an adult male of this species, Dr. F. C. Fraser has generously contributed notes and a sketch (fig. 11) describing the structure of alveoli of the jaw of an adult male on exhibit in the British Museum (Natural History). "On the left ramus of the mandible the area of the alveolus is distinguished by irregularly pitted bone the outer margin of which is ill-defined but roughly pyriform in shape and measures 41.2 mm. long and 27.2 mm. wide. The stem end of this pear-shaped alveolar area is directed posteriorly and narrows sharply to connect with the persisting linear vestige of the mandibular toothrow (see fig. 6). On this left ramus there is a central cavity in the alveolus surrounded by the irregularly pitted bone. The somewhat egg-shaped margin of the central cavity measures 13.5 mm. long, 9.1 mm. wide, and 6.6 mm. deep. The walls of this central cavity are finely ridged, the ridges descending focally from the external margins of the cavity toward the deepest point. The deep smaller pits around the central cavity occur also around the right tooth. A seeker could be passed into some of them quite far, and they may be nutrient foramina. Although the base of the tooth seems to be resting on the irregularly pitted surface of the right alveolus and no central cavity can be seen beneath the tooth, the latter is firmly wired down to the jaw so that presence or absence of a central cavity remains uncertain."

Central cavity or not, the right tooth appears (to me as well as to Dr. Fraser), by its shape, to be evidently resting upon the shallow irregularly pitted surface of the alveolus, not imbedded in the bone. Even from this somewhat equivocal sample of one, I am encouraged by the similarity of structure of the teeth of *Hyperoodon ampullatus* to those of *Tasmacetus shepherdi,* to predict that when the alveoli of other adult males of *H. ampullatus* are examined they will also be

FIG. 12. Dorsal view of alveoli of immature specimen of *Hyperoodon ampullatus,* FMNH 15553. Left alveolus is natural; right alveolus has some artificial filling in which a tooth was once set while the skeleton of this specimen was on exhibit; some artificial material separates the rami; a nut is seen for a bolt holding the rami together.

found to have filled up the deep alveolus of immaturity with cancellus bone. The tooth will presumably be imbedded in tough connective tissues of the gum, with only a small part of the tip erupted and wearing off. The specimen of an immature of *H. ampullatus* in Chicago (FMNH 15553) has an alveolus adequately deep (fig. 12) to accommodate teeth up to 35 mm. long without erupting them through the gum if, as I assume, there is about 5 mm. of tissue separating the tooth from the bone in the alveolus, and about 10 mm. or more of tissue covering the bone externally. (The degree of immaturity of FMNH 15553 is indicated by the fact that on its mounted skeleton the sutures separate the epiphyses from the centra very openly on the thoracic, lumbar, and most of the caudal vertebrae, and that the epiphyses at both ends of the humerus, radius, and ulna are still free.) If such an individual were male, presumably in life the tooth would be gradually extruded from the alveolus and the latter filled up beneath it during the course of morphological maturation. If it is correct to assume, as the present investigator does from the sheer planing off of the apex by wear, that the margin of wear is essentially the gum line, then the gum would need to become about 30 mm. thick to accommodate a tooth so extruded as that in Figure 6.

For those species which are now best known of the genus *Mesoplodon,* in the adult male just as in the adult female and immature, the roots of the large pair of teeth remain long, and they remain sheathed in deep alveoli which thus do not fill with cancellous bone. Fraser (1946, fig. 11) has illustrated this for an adult male of species *bidens* by photographs of the lower jaw with tooth *in situ* and the mate of the tooth separate and posed well to show how deeply the root of the other is sheathed in the jaw. Raven (1942, figs. 4, 13, 16) and Moore (1958, figs. 4, 5) illustrate from both front and side the jaws of adult males of species *densirostris* with teeth *in situ* and then the teeth separately, permitting one to observe that about 75 mm. of the 150 mm. length of tooth may fit into the alveolus. In van Beneden and Gervais (1880, pl. 24, figs. 2, 2a, 3b) and Moore (1960, figs. 1, 2, 4) one observes that the teeth of adult males of *europaeus* may be sheathed in the alveolus for half or more than half of the length of the tooth. Flower (1878, pl. 72, fig. 3) and Lydekker (1911, fig. 138) provide some indication of this depth of alveolus for adult male specimens of *grayi* (see also fig. 3). True (1910, pl. 12) and Moore (1963b, figs. 6, 8, 9, 10) show somewhat better how much of the length of the tooth fits into the deep alveolus in adult males of *stejnegeri,* and the latter (op. cit., fig. 12) shows the tooth of the type specimen of *bowdoini* in place in a lateral view of the mandible. Harmer (1924, pl. 3) presents a photograph of the lateral view of the mandible of the only known fully adult male of *mirus* with the teeth *in situ* so that one can see how much depth of jaw there is for the teeth to be sheathed in, but he did not take a tooth out to reveal the length of its root. Above it is reported that, although its teeth are still unknown, the alveoli of an adult, presumed male of *pacificus* are 26 mm. deep. These are proportionately the shallowest alveoli attributed to the genus *Mesoplodon*, and indeed provide the first good evidence for separating this species from that genus. Nishiwaki and Kamiya (1958, pl. 5, 10) show that about half of the length (apex to root) of the tooth in the adult male type of *ginkgodens* is sheathed in the bony socket of the cleaned jaw. Moore (1963b, figs. 8, 15) reveals that the deep alveolus of the adult male type specimen of *carlhubbsi* accepts about a third of the length of its (133 mm.) tall tooth. Thus, the alveoli of morphologically mature males of nine species of *Mesoplodon* evidently remain much deeper in proportion to the length of the tooth than is observed in the other genera.

At the primitive end of a primitive-derivative gradient constructed on alveolar characteristics alone, we place *Tasmacetus* and *Berardius* together because the alveoli of males and females are presumed (in *Tasmacetus*) or known (in *Berardius*) to be alike, whereas in other genera sexual dimorphism is exhibited in the characteristics of the alveoli of adults. Alveoli of *Tasmacetus* seem to me to be more primitive than those of *Berardius* because those of the three *Tasmacetus* examined are shallower in proportion to length of tooth.

Among the three genera which are relatively derivative because they exhibit sexual dimorphism in characteristics of the alveoli, *Ziphius* may be placed nearest the primitive end of the scale. This is because the alveoli in males of *Ziphius* that are morphologically quite mature show that their alveoli become exceedingly shallow and may even form sponge-like bone pads similar to those of *Tasmacetus.* (See illustrations by True, 1910, pl. 23, figs. 1, 2.) Scarcity of evidence on the alveoli of adults of the species of *Hyperoodon* weakens any assessment of where *Hyperoodon* may belong on the gradient of most primitive to most derivative alveoli, but even on this weak evidence it seems better tentatively to regard it as more derivative than *Ziphius*.

Mesoplodon, because of the deep alveoli sheathing long roots of teeth of its morphologically mature males, belongs at the most derivative end of a scale based on alveoli. In the end then, if the assumptions made are correct, these alveolar characteristics give us

Tasmacetus, Berardius, Ziphius, Hyperoodon, and *Mesoplodon* as the order of most primitive to most derivative, and the greater gaps between them should come between *Berardius* and *Ziphius* and between *Hyperoodon* and *Mesoplodon.*

The alveoli of the type and only adult specimen of *Mesoplodon pacificus* Longman, 1926 have led me to believe that it represents a male, and because their depth is only 26 mm., which is proportionately very much shallower than those of other adult male specimens of the species of *Mesoplodon,* I have expected that the second specimen would require creation of a new genus. After this paper was some months in press, Dr. Maria Luisa Azzaroli of the University of Florence, Italy, sent me photographs for identification of a skull of an immature individual of *M. pacificus* Longman from the Somali Coast. The dorsal surfaces of the vertex of this skull are natural; whereas those of the type specimen are badly abraded. The differences in the shapes of the nasal bones and premaxillary crest on the Somali skull support the evidence from the alveoli of the type that this species is generically distinct. The following name is therefore suggested:

Indopacetus new genus

Type species.—Mesoplodon pacificus Longman, 1926.

Distribution.—Queensland east coast at MacKay, Somalian east coast at Danane.

Description.—A beaked whale known only from two skulls, which are distinguished by: 1) a deep horizontal groove in the maxillary bone just above the orbit; 2) premaxillary crest with extremely short posterior processes; 3) nasal bones which neither project forward midsagittally where they meet at the anterior edge of the vertex, nor are grooved by a deep-walled sulcus there, but are only slightly indented there by the flat surface of each nasal sloping slightly toward the middle. See also: "Generic Diagnoses" and "Key for Characters of the Skull."

THE ELEVATED SYNVERTEX

One of the characters of the skull that distinguishes the living genera of beaked whales (Flower, 1872, p. 204) is that bones of the cranium behind the superior nares are elevated so as to form a prominence or crest at the vertex of the skull. Flower (1872, p. 204) lists seven skull characters as common to the living genera of beaked whales then known. More recent discovery of a new living genus, *Tasmacetus* Oliver, 1937, belonging in the beaked whale family, has reduced those familial characters of the skull which still apply to all living genera to five. Of these five, the elevation of the vertex is the most conspicuous. For the living genera of the family, this character may be further defined: when the skull is upright and the long axis of the beak is horizontal, the premaxillary bones rise behind the superior nares until: 1) In lateral view their profiles at least reach the vertical (as in all but *Berardius*); or 2) When viewed from front or rear on the line of the long axis of the beak, the vertex stands so high above the supraoccipital that the profiles of the sides of the vertex are seen to be at least vertical (as in *Berardius* and *Tasmacetus*); or both 1 and 2 (as in *Tasmacetus*).

The vertex of a skull is by definition the highest point on it, but I find it useful in this family to coin a word synvertex (Greek prefix syn-, meaning together with) to include a small area usually elevated high above the rest of the skull, illustrated in Figure 13. The bones constituting this specially-elevated synvertex characteristic of the *Hyperoodontidae* are: 1) The nasal bones are usually the most central, but when short may share this location with an intrusion of both frontals from posteriorly; 2) The upturned posterior extremities of the premaxillary bones generally form most of the front of the synvertex. Here the premaxillaries are separated narrowly or widely by the nasals, and insert a narrow posterior process of bone alongside each nasal; 3) The thin layer of maxillary plate usually rises vertically to form the sides of the synvertex; 4) The supraoccipital rises high enough in most species to contribute the back edge of the synvertex, and it often forms an irregularly median wedge which spreads the frontals mildly; 5) The frontals usually form the smallest or least conspicuous part of the synvertex, posterior to the nasal bones.

An important feature across the front of the synvertex is the premaxillary crest. This is principally formed by the *widening* of the upturned posterior ends of these bones, but in many species there is also a *thickening* of the premaxillaries, and in some a pronounced curling forward of its top.

The Premaxillary Crests

In *Berardius* the postnarial ascension of the premaxillary bones to the synvertex does not reach or even approximate an angle perpendicular to the long axis of the beak-like rostrum. This is the only living genus of the *Hyperoodontidae* for which this is true, and since this condition of *Berardius* is nearer the common one of other Ceta-


a
b
c
d
e

FIG. 14. Left lateral view of synvertex of skull of *Berardius arnuxi*, DM 183, illustrating the characteristic unique among living genera of beaked whales that the profile of neither premaxillary bone rising to the synvertex reaches a position perpendicular to the long axis of the beak.

cea, *Berardius* is to be regarded as less derivative than the other hyperoodontid genera in this respect. This characteristic is illustrated in Figure 14 in which the long axis of the beak of the specimen and of the camera frame were carefully ascertained to be horizontal for this photograph. That the axis of the beak would therefore be parallel to the horizontal edges of the finished halftone has been checked against the frame of the original negative. Another distinctive characteristic of the elevated synvertex in *Berardius* is the exceedingly small amount of either widening or thickening of the elevated posterior extremities of the premaxillary bones (fig. 19) where these dimensions constitute by definition what little there is of a premaxillary crest.

In *Ziphius* there is little or no thickening of the upraised posterior ends of the premaxillaries to contribute to a premaxillary crest. The

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FIG. 13. Synvertex of the skull of *Mesoplodon grayi*, an adult ♀, USNM 49880: right premaxillary bone (a), right nasal bone (b), right frontal bone (c), right maxillary bone (d), supraoccipital bone (e) fused with both frontal bones. This shows how the premaxillary crest is wide and thick, that the nasal bones extend farthest forward at the side, and that a sulcus, U-shaped in cross-section, extends down the front of the combined nasal bones.

FIG. 15. Dorsal view of synvertex of skull of *Ziphius cavirostris*, FMNH 99362, showing the premaxillary bones (a) to be narrow and thin but strongly turned forward, and the nasal bones (b) to extend farthest forward mesially. Also marked are: right frontal bone (c), right maxillary bone (d), and supraoccipital bone (e).

left premaxillary narrows rather than widens, and although the right one does widen, it is so incipient, so feebly developed, that, as in *Berardius*, it would hardly be called a crest but in deference to its better development in the other genera. There is development in the premaxillary crest of *Ziphius* which is peculiar to this genus: both the right and left parts of the crest are turned so that the anterior fronts of the crest face inward some 30 to 45° from straight forward, as shown in Figure 15.

In *Tasmacetus* there is a substantial widening of the upraised ends of both premaxillary bones to form a more respectable premaxillary crest (fig. 17) than is found in either *Berardius* or *Ziphius*. The middle of the anterodorsal edge of the upcurled posterior end of each premaxillary does also thicken notably, so that both parts of the two-parted premaxillary crest do in *Tasmacetus* develop this second component which characterizes the more fully developed crests in relatively derivative genera.

In *Indopacetus* the lateral expansion of the ends of the premaxillary bones to form the premaxillary crests exceeds that observed in

Tasmacetus and also that observed in *Mesoplodon hectori.* The posterior process of each side of the premaxillary crest extending alongside the nasal (illus. for *Mesoplodon stejnegeri* by Moore, 1963, fig. 3) is poorly developed and far shorter than in *Tasmacetus.* The right and left parts of the crest are also thickened anteroposteriorly. The form of the premaxillary crest is not penetrated and contributed to by an anterior process of the nasal as in *Mesoplodon* and *Hyperoodon.* In lateral view like that of *Tasmacetus* the profile of the premaxillary crest of *Indopacetus* barely rises to vertical to the long axis of its beak.

In *Mesoplodon* the upturned, postnarial part of the premaxillaries widens and thickens prominently in each of the living species, although in *hectori* the thickening is both more pronounced than the widening and located separately above the widened part on both bones, so that *thickening* characterizes only the higher part of the premaxillary crest and widening only the lower (Fraser, 1950, pl. 3, figs. 1, 2). In the genera *Mesoplodon* and *Hyperoodon* the part of the premaxillary crest formed by the right premaxillary bone accepts *into its own form* an intrusion of the lateral process of the right nasal

FIG. 16. Dorsal view of synvertex of skull of *Hyperoodon ampullatus*, FMNH 15553, immature, showing: very wide development of premaxillary (a) in crest; extreme thickness of premaxillary in crest; greatest participation of nasal bones (b) in the premaxillary crests by penetration of the very form of each premaxillary and partial replacement of it; the U-shaped depression in the combined nasal bones is wide and shallow in this immature specimen but becomes narrow and deep in adults (Gray, 1846, pl. 4); the wide sutures facilitate distinction of frontal bones (c), maxillary bones (d), and the supraoccipital (e).

bone. In many but not all species of *Mesoplodon* and *Hyperoodon* the lateral process of the right nasal extends quite far forward into the premaxillary crest. Examples best illustrated are *M. europaeus* (Raven, 1937, fig. 8), *M. layardi* (Hale, 1931, fig. 20), *M. hectori* (Fraser, 1950, pl. 3, fig. 1), *M. grayi* (fig. 13, the present paper), *M. ginkgodens* (Nishiwaki and Kamiya, 1958, pls. 3, 4), and *M. carlhubbsi* (Moore, 1963b, fig. 13).

In *Hyperoodon ampullatus* the widening and thickening of the premaxillary crest is as fully developed (fig. 16) as in any species of *Mesoplodon*, and this is true also of *H. planifrons*. In this genus, also, occurs the derivative extreme in the premaxillary crest for consistent curling forward far over the nares. For characters of the premaxillary crest, therefore, *Hyperoodon* represents the derivative extreme of the living genera of its family.

From the most primitive to the most derivative in characters of the premaxillary crests the genera should therefore be arranged as follows: *Berardius, Ziphius, Tasmacetus, Indopacetus, Mesoplodon, Hyperoodon*. *Berardius* and *Ziphius* are most distant from each other and about equally from *Tasmacetus*. *Mesoplodon*, with its many species, bridges the differences between the premaxillary crests of *Tasmacetus* and *Indopacetus* and those of *Hyperoodon*, the most primitive of *Mesoplodon* (*hectori*) resembling the former, the most derivative (*carlhubbsi, bowdoini, layardi*) resembling *Hyperoodon ampullatus*. *Ziphius* has developed in a different direction from the other genera in the form of its premaxillary crests as well as that of its nasal bones.

The Nasal Bones

Centrally located on the synvertex of the skull, the paired nasal bones also extend anteriorly and down from the synvertex to the mesethmoid bone (fig. 17) which, like the anterior faces of the nasals, provides part of the posterior wall of the superior nares. The right nasal bone is the larger of the pair throughout the living members of the family; it is generally wider, reaches higher, and its lateral process (present in *Mesoplodon* and *Hyperoodon*) projects anteriorly farther than does that of the left nasal. The configuration of the nasals as

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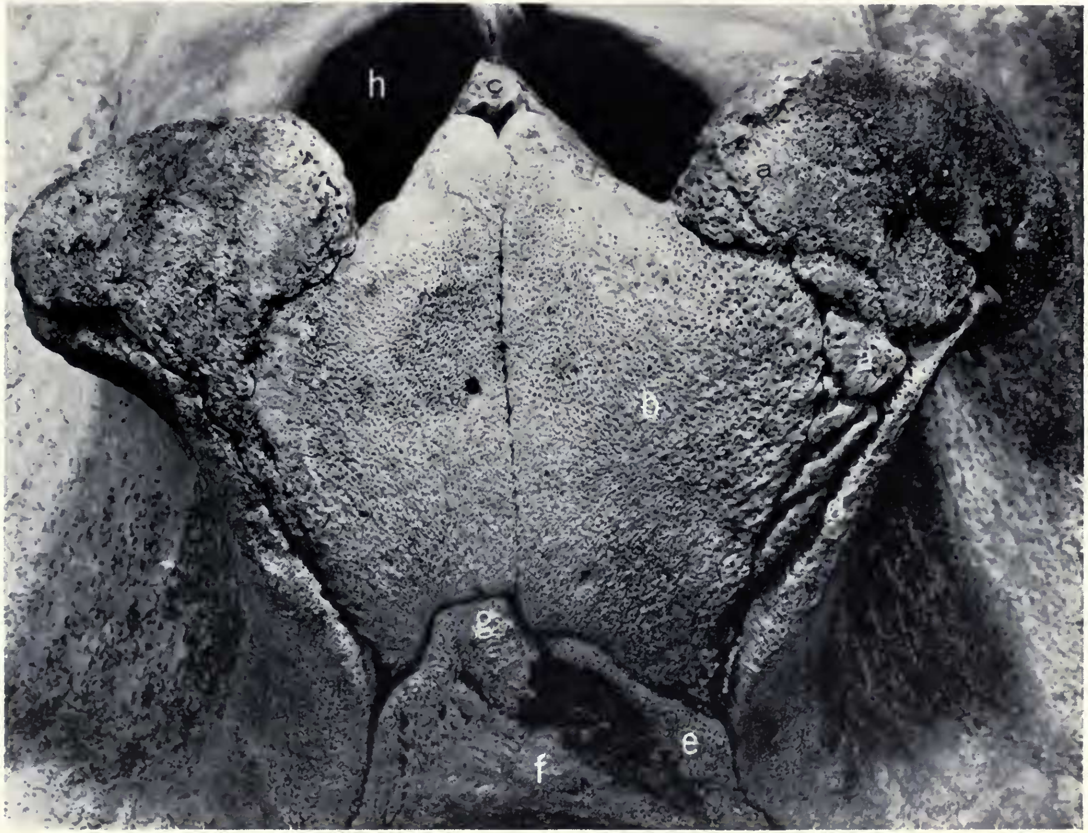
FIG. 17. Dorsal view of synvertex of skull of *Tasmacetus shepherdi* revealing the considerable widening of the premaxillaries to form the crest, and the nasals showing neither a deep median sulcus nor a median anterior projection on the (level of the) synvertex. Right premaxillary bone (a), right nasal (b), mesethmoid (c), right maxillary bone (d), right frontal bone (e), supraoccipital bone (f), left frontal (g), left naris (h). Photo courtesy of Dr. George Knox, UCM 1063.


h
c
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a
c
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f

they rise from the mesethmoid to the synvertex is markedly different in two groups of the genera of the family of beaked whales.

In *Tasmacetus:* 1) Where the nasal bones approach the anterior margin of the synvertex of the skull, they may be observed to be flat in postero-dorsal view. There is no most-anterior projection of the nasal bones; the middle and the sides are about equally anterior. 2) In their ascent from the margin of the mesethmoid bone to the synvertex, the nasal bones incline posteriorly from the vertical and reveal in lateral view a virtually flat profile (fig. 18). 3) At the anterior margin of the synvertex the premaxillae project farther forward than do the nasal bones.

In *Indopacetus:* 1) At the anterior extremity of the dorsal surfaces of nasal bones on the synvertex of the skull, they are slanted inward toward the suture between them, resulting in a slight indentation in their anterior margin, and permitting the lateral extremity of the right nasal to project slightly farther forward than any other part of the nasal bones on the surface of the synvertex. 2) In lateral view the profile of the right nasal bone rises from obscurity in the nares on a nearly straight line just perceptibly slanting posterior of vertical (to the long axis of the beak). 3) At the anterior margin of the synvertex the premaxillae project farther forward than do the nasal bones.

In *Berardius:* 1) Where the anterior surfaces of the nasals approach the synvertex, in dorsal view they are seen to be convex, and the most anterior projection of the nasal bones is at their mesial margins, where they meet (fig. 19). 2) In their rise from the margin of the mesethmoid bone to the synvertex, the profile of the nasal bones rises vertically at first then declines progressively to the rear, and so in lateral view is seen to be convex. 3) At the level of the premaxillary crests the nasal bones project anteriorly farther than do the crests.

In adults of *Ziphius:* 1) In dorsal view the anterior face of the nasal bones becomes *convex* near the synvertex, and their most anterior projection is at, or nearly at, their mesial margins where they meet (fig. 15). 2) Ascending, the concave anterior faces of the nasals in lateral view incline *forward* from the vertical (when the skull is upright and the long axis of the beak is horizontal), then, a few centi-

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FIG. 18. Left lateral view of skull of *Tasmacetus shepherdi* illustrating its more derivative condition than *Berardius* in that the rise of the premaxillaries to the synvertex attains an angle vertical to the long axis of the beak: right premaxillary (a), left premaxillary (b), right nasal (c), left nasal (d), left maxillary (e), mesethmoid (f). UCM 1063.

FIG. 19. Dorsal view of synvertex of skull of *Berardius arnuxi* DM 183, illustrating the narrowness and thinness of the upturned ends of the premaxillaries (a), hence the most meager of premaxillary crests among the genera of beaked whales (compare with fig. 13), and that on the synvertex the nasals (b) extend farthest forward mesially. Also identified are the frontals (c), the maxillaries (d), and supraoccipital (e) bones.

meters before reaching the anterior margin of the synvertex, change to *convex*. 3) At the anterior margin of the synvertex of the skull the nasal bones project anteriorly separate from and farther than the premaxillary crests.

In *Hyperoodon:* 1) Where the anterior surfaces of the nasal bones reach the synvertex, a horizontal plane would transect their combined surfaces in a *concave* arc, and the most anterior projection of the nasals is near the *lateral* margin on the lateral process of the right nasal (see fig. 16). 2) In lateral view of the ascent of the nasals from the margin of the mesethmoid, the mesial portion of the anterior surfaces of both may be observed to incline slightly *posterior* of vertical. (The lateral portion of the anterior surface of each inclines *anteriorly* of vertical because a strong lateral process develops on each nasal and projects far anteriorly as part of the premaxillary crest.) 3) At the anterior margin of the synvertex the right premaxillary bone extends farther forward than does the lateral process of either nasal.

In *Mesoplodon:* 1) Where the anterior surfaces of the nasals approach the synvertex of the skull, they are seen in dorsal view to be strongly concave (i.e., a horizontal plane would transect their combined surfaces in a *concave* arc, or U-shape, as in fig. 13), and the most anterior projection of the nasals is near the lateral margin and on the lateral process of the right nasal. 2) In lateral view of the ascent of the nasals from the margin of the mesethmoid bone, the mesial portion of the anterior surfaces of the nasals inclines *posteriorly* from the vertical (and in some species does not reach the surface of the synvertex). 3) At the anterior margin of the synvertex one of the premaxillae (usually the right) ordinarily extends farther anterior than does either lateral process of the nasals.

From the characters of the nasal bones alone an arrangement of genera from most primitive to most derivative would start with development of two branches: the first branch would have *Berardius* on it as the more primitive and *Ziphius* as the more derivative; the second branch would have *Tasmacetus* on it as the most primitive and *Indopacetus, Mesoplodon,* and *Hyperoodon* as successively more derivative. Linearly, they can be arranged on a most primitive to most derivative scale as *Berardius, Tasmacetus, Indopacetus, Ziphius, Hyperoodon,* and *Mesoplodon,* but the former reveals the evidence of relationships better. *Berardius* and *Ziphius* resemble each other in characters 1, 2, and 3, and *Indopacetus, Hyperoodon,* and *Mesoplodon* also resemble each other in characters 1, 2, and 3. But the primitive two genera differ fully from the derivative three genera in characters 1 and 3. *Tasmacetus* is nicely intermediate in character 1 between the primitive two and the derivative three of the other living genera, and *Indopacetus* is close to intermediate. *Tasmacetus* resembles the more derivative pair of genera in character 3. In a general way the nasal bones of *Tasmacetus* seem somewhat intermediate in morphology between the primitive two genera, and, especially in dorsal view, most nearly resemble those of *Berardius.* The characters of the nasals of *Tasmacetus* can certainly be said to permit development equally well in the direction of nasals like those of *Ziphius* or toward ones like those of *Mesoplodon.* Concordance with the related differences of the premaxillary crest among these genera, however, suggests another interpretation: that the nasals of *Berardius* are the more primitive, and that those of *Tasmacetus* have already evolved slightly away from that state toward the characters typified by *Mesoplodon* and *Hyperoodon.*

Implications Regarding Relationships

Presentation of so much detail in two principal lines of evidence in this investigation of relationships among the living genera of beaked whales has proceeded farther than was contemplated at its inception, and beyond what I would have planned without including study of the fossil record. It grew as research tends to grow, by luring the student into exploring further lines of investigation that only become recognized as promising as the study proceeds. Now that exhaustion of time has drawn the line against further attractive possible lines of investigation my hope is that enough evidence has indeed been assembled and evaluated to establish the relationships of the living representatives of hyperoodontid phylogeny sufficiently to justify and stimulate a similar study of the fossils.

Although consideration of the teeth and alveoli has, compared with that of other lines of evidence, proceeded to greater length here and has revealed much of potential systematic value, these lines of evidence do not emerge as the most satisfying indicators of general degree of relationship observable in good samples of these genera available for study as museum specimens (usually skulls—often with mandible missing, still more often with the teeth missing). There is, for example, the practical objection to the small sample and imperfect knowledge of teeth and alveoli of adults of either species of *Hyperoodon*. While appreciation of taxonomic characteristics of the teeth and alveoli requires morphologically mature specimens, the taxonomic characters of the nasal bones and of the premaxillary crest described here, are well formed in immature specimens, which means that these characters have been observed, and are verifiable, in a much larger sample.

The number and position of teeth, the size and shape of teeth, and what is known of their alveoli, would all conspire to make *Ziphius* and *Hyperoodon* more closely related to each other than either is to any other genus. This is strongly opposed by evidence described in the characters of the elevated synvertex of the skull. In the characteristics of the nasal bones, *Ziphius* and *Berardius* more closely resemble each other than either does any other genus. In the characters of the nasal bones, also, *Hyperoodon* and *Mesoplodon* resemble one another more than any other genus. Moreover, on the synvertex also, the characters of the premaxillary crest firmly support the evidence from the nasal bones of close relationship between *Hyperoodon* and *Mesoplodon*. The premaxillary crest of *Ziphius* resembles that of *Berardius* more than of any other living genus in being both narrow and thin. The somewhat mesial orientation of the faces of the premaxillary crest, and also their erection to the vertical in *Ziphius*, indicate a separate line of development for *Ziphius* to a form clearly derivative; whereas the premaxillary crest of *Berardius* has remained exceedingly primitive. The long anterior development of the nasal bones of *Ziphius* may be said to support the evidence from the premaxillary crests of a more derivative condition of *Ziphius* than *Berardius*. (Also, characters 16 to 19 in the dendrogram may be considered four additional derivative ones of *Ziphius*, compared to which *Berardius* has primitive alternatives.)

In Flower's (1872) day, 65 years before *Tasmacetus* was discovered, drastic evolutionary reduction of the erupting teeth to only two pairs in one genus and a single pair in the other three living genera of beaked whales so strikingly distinguished the beaked whale superfamily from the other living Cetacea that only a few scientists gave weight to the other characters thought to distinguish the beaked whales. Only 30 years ago the discovery of *Tasmacetus* with long rows of functional upper and lower teeth, suddenly removed that previously convenient character.

Reconsideration of the characters distinguishing the living members of the superfamily from the remainder of the living Cetacea is outside of the scope of the present paper, but Fraser and Purves (1960, fig. 26) have recently contributed to knowledge of this superfamily distinction. However, the characters they use for this are evidently too constant within the superfamily to help me in the present investigation. In looking over the 15 superfamilial characters enumerated by Flower (1872, p. 204) for ones of the skull which have survived the discovery of *Tasmacetus*, I found the especially elevated synvertex of the skull to be the most impressive of the remaining skull characters of the living superfamily. Constituted by exposures of the upturned edges of four paired bones and one unpaired, it seemed complex enough to be likely to offer reward for intensive and quantified taxonomic investigations.

The above described and evaluated characteristics of the teeth and alveoli do not, for whatever reasons, now provide so convincing or coherent a basis for recognizing major phyletic divisions of the living genera of Hyperoodontidae as do the above described and evaluated characters of the synvertex of the skull. The latter are therefore employed with suitably primary emphasis in construction of the accompanying model (fig. 20) to depict, by interpretation of the above evidence, a hypothetical course of evolution which would ac-

FIG. 20. DENDROGRAM OF HYPOTHETICAL EVOLUTION OF LIVING GENERA OF THE BEAKED WHALES

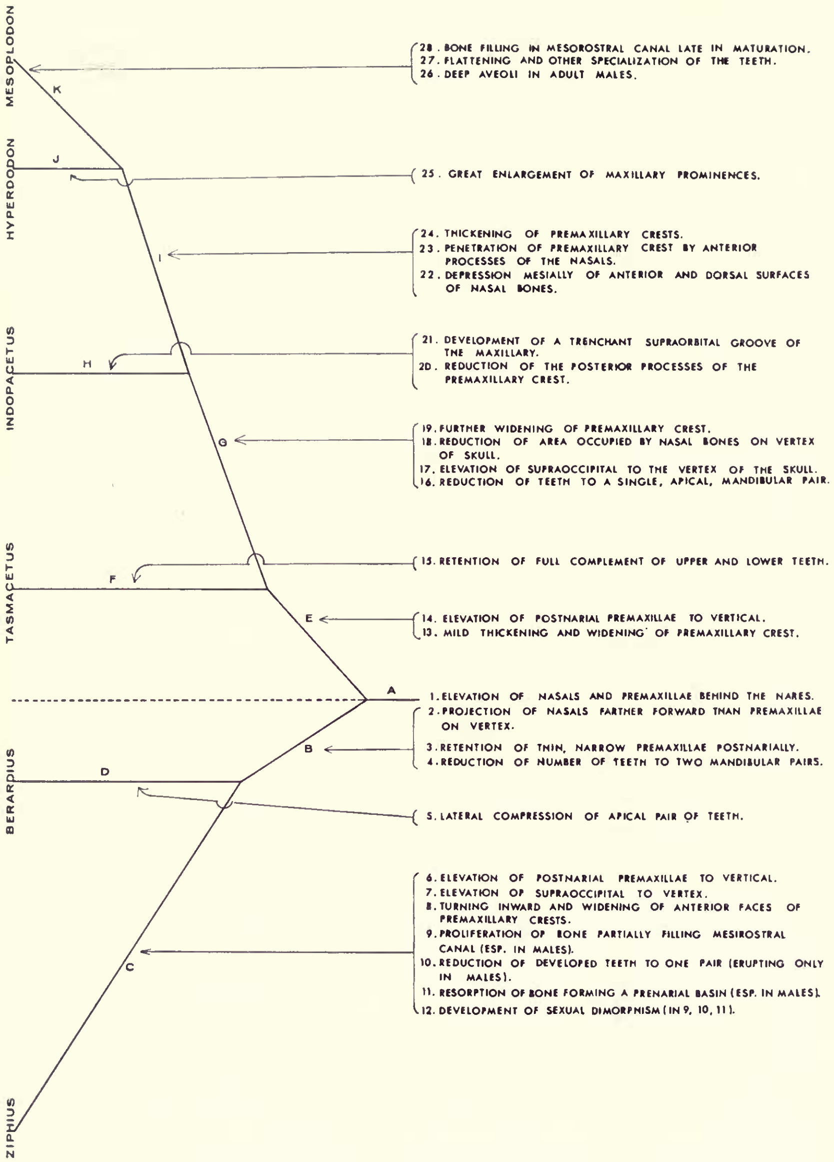

FIG. 20. Distance from any one generic name to each other along the hypothetical lines connecting them indicates degree of relationship between the genera (e.g., *Hyperoodon* and *Mesoplodon* are the most closely related of living genera, *Ziphius* and *Mesoplodon* the most distantly). A dotted line extended up to the "present" from lineage A provides a base line of primitiveness in the family from which the relative direct distances to the living genera expresses derivativeness.

count for the amount of observed difference among the six living genera.

The dendrogram is turned 90° from normal position to accommodate listing beside it the morphological characteristics basic to it.

Each hypothetical lineage in Figure 20 from which at least one living genus is supposed to have derived is designated by a letter. Lineage A represents ancestors to all the living genera of beaked whales. It is presumed to have had: the nasal and premaxillary bones notably elevated behind the nares, and (by implication of nos. 2, 3, 4, 8, 13, 14, and 18) the nasal bones neither sunken back nor projecting forward mesially at their anteriormost margin on the synvertex; nasals occupying most of the area of the synvertex; the premaxillae thin and narrow postnarially; numerous cone-shaped, functional, teeth on maxillae and mandible; premaxillae not achieving a postnarial rise perpendicular to the long axis of the beak; and the postnarially up-curved ends of the premaxillae very slightly widened to form an incipient premaxillary crest.

Lineage B is supposed to have differentiated in the following characteristics before giving rise to phyla C and D: the nasal bones projecting anteriorly from their common middle at the anterior margin of the synvertex; the maxillary teeth lost and the mandibular teeth reduced in number, perhaps to two apical pairs.

Lineage E presumably evolved the following characters before giving rise to lineages F and G: elevation of the premaxillae posterior to the nares until in profile they attain an angle perpendicular to the long axis of the beak, and mild widening of the premaxillary crest.

Lineage G, before proliferating phyla H and I, would have, as did B, experienced a great reduction in number of functional teeth; the supraoccipital would have, as in phylum C, risen approximately to the synvertex of the skull; on the synvertex of the skull the premaxillaries would by thickening and widening have expanded the relative area of the synvertex occupied, leaving the nasals comparatively less.

Lineage I, before giving rise to those two phyletic lines which have produced the living genera *Hyperoodon* and *Mesoplodon*, would have developed two new characteristics in the shape of the nasal bones: the middle of the common antero-dorsal surface of these paired, adjacent bones becomes recessed by a depression which is U-shaped in cross-section (fig. 13) and usually deepest at the meeting of the anterior and dorsal surfaces of these bones. This results in the lateral portion of each nasal bone being the part which reaches farthest forward on the synvertex of the skull, but this most forward-reaching part develops into an anterior process which penetrates the adjacent premaxilla and shares with it the form of the bipartite premaxillary crest (fig. 16).

Characteristics Considered Convergent

Several relatively derivative characteristics have, according to the hypothetical relationships depicted in Figure 20, been acquired independently, sometimes by quite divergent lineages. From relatively primitive to derivative in the dendrogram these would be:

Great reduction of number of teeth, in lineages B and G.

Elevation of the profile of the premaxillae postnarially until at least perpendicular to the long axis of the beak, in phyla C and E.

Elevation of the supraoccipital bone approximately to the synvertex of the skull, in lineages C and G.

Proliferation of bone, from at least the vomer, tending to fill the mesorostral canal, and thus to stengthen the slender beak, in phyla C, F and K.

Compression of the principal, or only, pair of well-developed teeth, in phyla D and K.

Sexual dimorphism in the eruption and degree of development of a single pair of teeth, in phyla C and I.

Sexual dimorphism in the degree of filling of the mesorostral canal in phyla C and K.

None of the lines of evidence pursued in the present investigation happens to include clear reference to the extraordinary character which distinguishes *Hyperoodon* as a genus, and in the males of *H. ampullatus* reaches a morphological development which seems to me the most amazing in the superfamily. This is the development of the pair of common, maxillary prominences into massive, soaring superstructures. (It probably has to become familiar to be appreciated. To a student of cetology they rival the antlers of the fossil "Irish elk" in magnificence, but whale skulls are extraordinary in so many ways that the special grandeur of the maxillary crests of an old male *H. ampullatus* may be beyond the immediate grasp of the uninitiated.) Thus, *Hyperoodon* does have this one very distinctive specialization. It does not, even so, quite equal *Mesoplodon* in derivative characteristics in all the lines of evidence studied, and particularly, of course, in the dentition which seems especially important at the generic level in beaked whales (but also at infrageneric levels), as indicated in characters 8, 9, and 10 with the dendrogram.

DISCUSSION OF CLASSIFICATION

Inasmuch as Simpson (1945, p. 215) wrote almost regretfully of having accorded the beaked whales only familial status instead of superfamilial, and since Fraser and Purves (1960, fig. 26) raised them to superfamily rank, use of the superfamily category is followed here.

The dendrogram illustrates the relationships between the two major divisions of the genera of Hyperoodontoidea, and tribal rank for these in classification is required to acknowledge the differences between them so that there will still be a lower suprageneric category to express the much greater differences between *Tasmacetus* or *Indopacetus* and either *Hyperoodon* or *Mesoplodon* than exist between the latter two. The tribes Hyperoodontini to include *Tasmacetus, Indopacetus, Hyperoodon,* and *Mesoplodon*; and Ziphiini to include *Berardius* and *Ziphius,* do permit the other differences that are greater than generic to be expressed with subtribal rank, and this is done.

Simpson (1945, p. 215) in his most recent classification of the mammals followed principally Kellogg (1928) in his arrangement of the beaked whale genera, which of course contains the fossil ones, but concluded that no satisfying arrangement of the genera within the family had yet been achieved. Fraser and Purves (1960, p. 40) whose intensive research on the living Cetacea included *Berardius* (2 species), *Ziphius* (1), *Hyperoodon* (1), and *Mesoplodon* (1) as their sample of the beaked whales, found the sample to be remarkable among the Cetacea as a whole because there was a "general homogeneity . . . of structure in this region [the basicranial region affected by specialization for underwater hearing] in all the ziphioids, there being little or no evidence of progressive changes between individual [genera]." It is true that Scheffer and Rice (1963) and Hershkovitz (1966, p. v) offer compilations with arrangements of those genera which they doubtless hope to be natural. It is also correct that both arrangements recognized *Tasmacetus* as especially primitive and *Hyperoodon* as much more derivative, but there is no other concordance with the present findings nor, of course, any evidence offered that justifies those arrangements of the taxa. Thus, no previous student

FIG. 21. *Hyperoodon (Hyperoodon) ampullatus*, FMNH 15553, front view, sighted between maxillary crests (a), with long axis of beak horizontal, camera leveled and with center of lens at height of summit of mesethmoid bone (b), revealing how even in this very immature specimen the maxillary prominences are crests soaring above the mesethmoid bone. Premaxillary bones (c) and nasal bones (d) also shown.

of cetacean systematics has from original research offered a classification of the living genera of beaked whales with which the present offering needs to be reconciled. A very real gap in knowledge of relationships among living genera therefore exists which the present paper seeks to fill.

In the above analysis of "Relationships Among the Genera" there was little need to deal with infrageneric categories except in species of *Mesoplodon*, but the species *Hyperoodon planifrons* and *H. ampullatus* are so exceedingly distinct from one another in the very character that most distinguishes them both from other genera, the enormous enlargement of the maxillary prominences, that subgeneric distinction is appropriate. Since *ampullatus* is the type species of the genus and no generic or subgeneric name has been proposed for *H. planifrons*, a new subgeneric name is proposed.

Frasercetus new subgenus

Type species.—Hyperoodon planifrons Flower, 1882. The maxillary prominences in *Frasercetus*, although massive, are low, spreading, and do not rise to the height (above the long axis of the beak) of the vertex of the skull. In subgenus *Hyperoodon* the maxillary prominences stand erect as great crests even in immatures (fig. 21), and in adult males rise high above the synvertex of the skull (Gray, 1846, pl. 4).

The new name recognizes Dr. F. C. Fraser of the British Museum for his many contributions to our knowledge of beaked whales, and other Cetacea, several references to which should be found in the literature cited.

Scheffer and Rice (1963, p. 8) placed several big-toothed species in the subgenus *Dioplodon*, but unpublished plots of my measurements of teeth of more than 80 adults of 11 species of *Mesoplodon* show no adequate basis in the size of teeth for breaking up the species of *Mesoplodon* into a large-toothed subgenus and a small-toothed one. Size of teeth among species of *Mesoplodon* being therefore an irrelevant continuum one must abandon it, and classify the species instead in a most-primitive-to-most-derivative progression on the characteristics (described in detail above): 1) distance of alveolus from apex of mandible; 2) anteriorly inclining, erect, and posteriorly inclining posture of tooth; and 3) orientation of the denticle on the tooth.

While there is, in the evidence available to me, no break or gap in tooth size sufficient to warrant separation into a subgenus of several species with big teeth, and another of several with little, two species of *Mesoplodon* are individually regarded as subgenerically distinct in morphological characters as follows: extraordinary width and depth of the jaw especially, but the teeth somewhat massive also, in *densirostris*; the exceedingly derivative character of the teeth in *layardi* as described above. Names *Dolichodon* and *Dioplodon*, respectively, are available and employed.

For synonymies and detailed records of distributions with citations, see Hershkovitz (1966, pp. 122–149).

CLASSIFICATION OF THE LIVING GENERA OF BEAKED WHALES

Order	CETACEA Brisson, 1762, pp. 3, 227 (=Cete Linnaeus, 1758, p. 75). Whales, porpoises, dolphins.
Suborder	ODONTOCETI Flower, 1867, pp. 110, 115. Toothed whales.
Superfamily	HYPEROODONTOIDEA, new name. Beaked whales.
Family	HYPEROODONTIDAE Gray, 1866, p. 62. Beaked whales.
Tribe	ZIPHIINI, new form?
Subtribe	BERARDIINA, new form. Four-toothed whales.
Genus	*Berardius* Duvernoy, 1851.
Species	*Berardius arnuxi* Duvernoy, 1851. Southern four-toothed whale. Temperate waters of the southern hemisphere.
	Berardius bairdi Stejneger, 1883. Northern four-toothed whale. North Pacific temperate waters.
Subtribe	ZIPHIINA Gray, 1850, pp. 56, 61 (greatly restricted). Goose-beaked whales.
Genus	*Ziphius* G. Cuvier, 1823.
Species	*Ziphius cavirostris* G. Cuvier, 1823. Goose-beaked whale. Warm and temperate waters of the world (provisionally charted by Moore, 1963a).
Tribe	HYPEROODONTINI, new form.
Subtribe	TASMACETINA, new form.
Genus	*Tasmacetus* Oliver, 1937. Tasman whale.
Species	*Tasmacetus shepherdi* Oliver, 1937. Tasman whale. New Zealand waters.

Subtribe	INDOPACETINA, new form.
Genus	*Indopacetus*, new genus.
Species	*Indopacetus pacificus* Longman, 1926. Indo-Pacific whale.
Subtribe	HYPEROODONTINA, Gray, 1846, part.
Genus	*Hyperoodon* Lacepede, 1804. Bottle-nosed whales.
Subgenus	*Hyperoodon* Lacepede, 1804.
Species	*Hyperoodon ampullatus* Forster, 1770. Northern bottle-nosed whale. Very northern North Atlantic.
Subgenus	*Frasercetus*, new subgenus.
Species	*Hyperoodon planifrons* Flower, 1882. Southern bottle-nosed whale. South temperate and southern subtropical waters.
Genus	*Mesoplodon* Gervais, 1850. Deep-socketed whales.
Subgenus	*Mesoplodon* Gervais, 1850.
Species	*Mesoplodon hectori* Gray, 1871. Southern hemisphere temperate waters.
	M. mirus True, 1913. Predominantly northern North Atlantic (charted by Moore, 1966).
	M. europaeus Gervais, 1855. Antillean beaked whale. Southern North Atlantic (charted by Moore, 1966).
	M. ginkgodens Nishiwaki and Kamiya, 1958. Ginko-toothed whale. Southern North Pacific and Indian Ocean (see Moore and Gilmore, 1965).
	M. grayi von Haast, 1876. Scamperdown whale. Southern hemisphere temperate waters.

	M. carlhubbsi Moore, 1963. Arch-beaked whale. North Pacific waters (charted by Moore, 1963b).
	M. bowdoini Andrews, 1908. Deep-crested whale. Southwest Pacific and Indian Ocean.
	M. stejnegeri True, 1885. Bering Sea beaked whale. Northern North Pacific (charted by Moore, 1963b).
	M. bidens Sowerby, 1804. North Sea beaked whale. Northeastern North Atlantic (charted by Moore, 1966).
Subgenus	*Dolichodon* Gray, 1871.
Species	*M. layardi* Gray, 1865. Strap-toothed whale. Southern hemisphere temperate waters.
Subgenus	*Dioplodon* Gervais, 1850.
Species	*M. densirostris* Blainville, 1817. Dense-beaked whale. Tropical and warm waters of the world (discussed by Moore, 1966).

Characters of Suprageneric Taxa

The tribe Ziphiini, as is obvious in the above classification, includes genera *Berardius* and *Ziphius,* and in the dendrogram, Figure 20, hypothetical phyla B, C, and D. Its unifying and diagnostic characters as presently known from only the living genera are that the nasal bones project farther anteriorly from the synvertex than do the premaxillae (see figs. 15 and 19), and the posterior up-turned ends of the premaxillae are thin. The subtribe Berardiina as presently known contains only the living genus *Berardius* and will thus have the same diagnosis, given below.

The tribe Hyperoodontini includes the known members of living genera *Tasmacetus, Indopacetus, Hyperoodon,* and *Mesoplodon,* and in Figure 20 the hypothetical lineages E, F, G, H, I, J, and K. Its distinctive characters are definitely widened and thickened postnarial premaxillae, and projection of these anteriorly from the synvertex of the skull beyond the nasals (see figs. 13, 16, and 17). Subtribe Tasmacetina thus far contains only the living member of the genus *Tasmacetus*, and so has the same diagnosis, given below. Subtribe Indopacetina contains only the known living member of the genus *Indopacetus*, and so shares its diagnosis, given below. Subtribe Hyperoodontina includes all of the 13 known living species of *Hyperoodon* and *Mesoplodon*, and in the dendrogram the hypothetical lineages I, J, and K. This subtribe is characterized by a depression (U-shaped in cross-section) of the middle of the antero-dorsal surface of the combined nasals which permits the antero-lateral part of each nasal bone (but especially the right one) to project farther anteriorly than does the mesial part (see figs. 13 and 16).

GENERIC DIAGNOSES

Berardius Duvernoy, 1851, the four-toothed whales

Characteristics

1. In adults of both sexes (Omura, *et al.*, 1955, pp. 107, 108) there are two pairs of well-developed teeth, the larger pair at the apex of the mandible, a smaller pair a decimeter or two posterior to the first; the tips of both pairs protrude through the gum, and at least the anterior pair sustain wear. (Kirino, 1956, shows that 84.6 per cent of a sample of 65 adults of *bairdi* had only two pairs, none had less, and only 3.1 per cent had more than a single supernumerary tooth.) This character distinguishes *Berardius* from all other living genera of Cetacea. See Figure 22.

2. When the skull is upright and the long axis of the beak is horizontal, viewed laterally the dorsal profile of the premaxillary bones does not reach (in its posterior ascent) or even approximate, vertical. See Figure 14.

3. The suture between the maxillary and premaxillary bones does not fuse for more than 20 per cent of its length on the dorsolateral surface of the beak. (The suture was partly closed by fusion of these bones in *only* one instance, on both sides for about 10 per cent of the suture's length on the beak, and *at the anterior end.*)

4. When the skull is viewed from posteriorly on a line with the long axis of the beak, the synvertex (constituted in this genus by the dorsal surfaces of the nasal bones and ends of the premaxillaries) rises above the supraoccipital bone like a slightly domed cupola with sheer sides. (*Tasmacetus* is similar from this view, but its synvertex is flat or depressed instead of slightly dome-shaped.)

By the characters enumerated above, the sample of 31 skulls of *Berardius* is distinguished from the examined samples of the other living genera of beaked whales as follows: *Ziphius* by characters 1, 2, 3, and 4; *Tasmacetus* by numbers 1, 2, and 3; *Indopacetus* by 1, 2, 3, and 4; *Hyperoodon* by 1, 2, 3, and 4; and *Mesoplodon* by 1, 2, 3, and 4.

FIG. 22. Teeth of *Berardius bairdi*, adult ♂ 33 feet long (Pike, 1953), showing relative size of one of the larger, apical pair (which are triangular and laterally compressed) and one of the cone-shaped subapical pair. Larger tooth is 89 by 103 mm. Courtesy of Gordon C. Pike.

Ziphius Cuvier, 1823, the goose-beaked whale

Diagnosis

1. Where the premaxillary bones ascend posteriorly on either side of the superior nares and terminate, their anterior faces are oriented mesially a small but obvious amount from directly forward. See Figure 15.

2. The combined breadth of the nasal bones is greatest anteriorly and where the right nasal is out of contact with the right premaxillary bone. See Figure 15.

3. When the skull is upright and the long axis of the beak is horizontal, in lateral view the nasal bones both project somewhat farther anteriorly *from the synvertex* of the skull than do the up-curled posterior ends of the premaxillary bones. See Figure 15.

By all three of the characters enumerated above the 50 specimens of *Ziphius* examined differ from the cited samples of *Berardius, Tasmacetus, Indopacetus, Hyperoodon,* and *Mesoplodon.*

Tasmacetus Oliver, 1937, the Tasman whale

Characteristics

1. There is a row of functional maxillary teeth, numbering 21 or 22 to a side and measuring 15 to 27 mm. in length, 5 to 13 mm. wide

(in the two specimens), and a long row of functional mandibular teeth, numbering 25 to 27 on a side (in the three specimens). Anterior to the mandibular tooth rows, and separated from them on each side by a diastema 25 to 45 mm. long, is a pair of larger teeth at the apex of the mandible.

2. The greatest transverse breadth of the nasal bones on the synvertex of the skull exceeds the greatest transverse breadth of the right portion of the premaxillary crest. See Figure 17.

3. The greatest length of the posterior process of the right part of the premaxillary crest exceeds the remaining anteroposterior thickness of the crest; and the greatest length of the left one exceeds the remaining anteroposterior thickness of the left part.

4. When the long axis of the beak is horizontal, the supraoccipital is so low that if the skull is viewed from 2 or 3 m. on a line with the long axis of the beak, the widest part of the premaxillary crest stands above the profile of the braincase.

Diagnosis

By the characters enumerated above, *Tasmacetus* is distinguished from other living beaked whale genera as follows: from *Berardius* by 1 and 3; *Ziphius* by 1, 2, and 4; *Indopacetus* by 1, 2, 3, and 4; *Hyperoodon* by 1, 2, and 4; and *Mesoplodon* by 1, 2, and 4.

Indopacetus Moore, 1968, Indo-Pacific whale

Characteristics

1. The alveoli of the developed teeth are a single pair, apical on the mandible, and in an old adult male become progressively at least as shallow as 30 mm.

2. The frontal bones occupy an area of the synvertex of the skull approximating or exceeding that occupied by the nasal bones.

3. There is almost no posterior process of the premaxillary crest extending posteriorly on the synvertex between the nasal and maxillary bones, or between the frontal and maxillary bones.

4. In the lateral extension of the maxillary bone over the orbit there is a deep groove about half as long as the orbit.

5. At about the midlength of the beak there is a swelling caused by the lateral margins proceeding forward a short distance without convergence (in the Danane whale) or even with a little divergence (in the MacKay whale), then convergence again.

Diagnosis

Indopacetus is distinguished by the characters enumerated above from the other living genera of beaked whales as follows: *Berardius* by nos. 1, 2, 3, 4, and 5; *Ziphius* by 2, 3, 4, and 5; *Tasmacetus* by 1, 2, 3, 4, and 5; *Hyperoodon* by 2, 3, 4, and 5; and *Mesoplodon* by 1, 3, 4, and 5.

Hyperoodon Lacepede, 1804, the bottle-nosed whale

Diagnosis

1. When the skull is upright and the long axis of the anterior half of the beak is horizontal, a horizontal plane transecting the summit of either maxillary prominence passes well above the mesethmoid bone. See Figure 21. This distinguishes all 25 specimens of *Hyperoodon* from all of the above specimens studied of the other living genera of beaked whales.

2. The greatest length of the largest maxillary foramen exceeds the least distance between the paired premaxillary foramina in the same individual. This distinguishes all 25 specimens of *Hyperoodon* from all the other specimens studied of other genera of beaked whales as listed above (except one unusual individual out of 32 *Mesoplodon layardi*).

The specimens of *Hyperoodon* studied consisted of 21 *H. ampullatus* and four *H. planifrons.*

Mesoplodon Gervais, 1850, deep-socketed whales

Characteristics

1. The alveoli of aging males remain deep, in many species continuing to contain about half the length of the tooth, and in all species probably exceeding 30 mm. in depth. (This distinguishes all adult males of *Mesoplodon* examined as follows: *mirus,* 2; *europaeus,* 3; *ginkgodens,* 2; *grayi,* 6; *carlhubbsi,* 4; *bowdoini,* 4; *stejnegeri,* 3; *bidens,* 15; *layardi,* 6; and *densirostris,* 8. No adult male is yet known of *M. hectori.*)

2. The single pair of teeth of any adult *Mesoplodon* is so compressed transversely that the greatest diameter of the tooth perpendicular to the long axis of the tooth is at least 1.66 of the greatest transverse thickness of the tooth (which would be perpendicular to both the long axis and the axis of the preceding, anteroposterior dimension).

3. The suture between the maxillary and premaxillary bones fuses in adults for more than 50 per cent of its length on the dorsolateral surface of the beak.

4. In posterior view on a line with the long axis of the beak, the supraoccipital occludes the synvertex of the skull so much that sheer sides may not be seen on both sides of the premaxillary crest.

5. The anterior faces of the premaxillary bones rising beside and behind the superior nares, are both oriented anterolaterally or anteriorly, but not anteromesially.

6. The right nasal bone remains in contact with the right premaxillary bone anteriorly where the breadth of the combined nasals is greatest.

7. When the skull is upright with the long axis of the beak horizontal, and is viewed laterally, the premaxillary bones are seen to project anteriorly from the vertex of the skull farther than the nasal bones (comparing right premaxillary with right nasal, and left with left).

8. When the skull is upright with the long axis of the beak horizontal, a horizontal plane transecting the summit of either maxillary prominence passes well above the mesethmoid bone.

9. The least distance between the pair of premaxillary foramina exceeds the greatest length of the larger maxillary foramen in the same individual. (This distinguishes 184 of the 185 individuals of *Mesoplodon* here reported, the exception being one of the 32 *M. layardi.*)

Diagnosis

The genus *Mesoplodon* is distinguished from other living genera of beaked whales by the above-numbered characteristics as follows: from *Tasmacetus* by number 1; *Berardius* by 1, 2, 3, and 4; *Ziphius* by 5, 6, and 7; *Indopacetus* by 1 and 2; and from *Hyperoodon* by 8 and 9.

KEYS FOR IDENTIFICATION OF THE LIVING GENERA OF BEAKED WHALES

Several authors have published keys for identifying the genera of beaked whales of a particular part of the world, a recent example being that of McCann (1962a). Despite its broad title, "Key to the family Ziphiidae, beaked whales," this example proceeds to limit itself to species of living beaked whales then known to occur in New Zealand waters. This excludes the seven species of *Hyperoodon, Berardius,* and *Mesoplodon* known only to occur in the northern hemisphere. It also excludes *Mesoplodon hectori, I. pacificus,* and *M. densirostris,* the first two for reasons quoted, and I think invalidated, above, and *M. densirostris,* presumably because it is not known from New Zealand waters. *M. densirostris* has been known from Lord Howe Island for almost a century (Krefft, 1870), 700 miles west but hardly 3° north of New Zealand. The likelihood that this omission of *densirostris* as potentially a part of the New Zealand marine fauna will vitiate McCann's key to the local species of *Mesoplodon,* has now been emphasized by the occurrence of *densirostris* 9° of latitude farther south on a Tasmanian beach (Guiler, 1966), and by the implications assembled by Moore (1966, pp. 50–51) that *M. densirostris* may occupy habitat farther off-shore than do other species of *Mesoplodon.*

The following keys do propose to distinguish, one key by characters of the skull, the other by those of the teeth, all presently known living species of all these genera to the level of genus.

Beaked Whales in the Flesh

A whale examined in the flesh belongs to the beaked whale family if it: 1) is a small whale (from 4.3 – 12.8 m. long for adults); 2) has no notch dividing the caudal fin conspicuously into right and left flukes; 3) possesses a pair of natural grooves on the throat, convergent anteriorly but not connected; 4) has the rostrum narrow and produced anteriorly like a dolphin's beak; and 5) lacks plates of baleen (protruding down from the upper jaw with which to sieve small food from seawater taken into the mouth). Exceptions or modifications have been reported for items 2 and 3.

Although the species *Mesoplodon hectori* was discovered and made known to science almost 100 years ago, and was the fifth of 11 living species now of *Mesoplodon* to be described, the first adult specimen, as of this writing, has just been reported upon (Guiler, 1967). As *Indopacetus pacificus* is still known from but two skulls, the character of its external appearance remains to be discovered.

Sets of comparable external measurements of adults of *Ziphius cavirostris* and even for *Hyperoodon ampullatus,* as well as the rarely seen *H. planifrons,* are not available in the literature in sufficient number to permit construction of a key to the genera in the flesh. Part of the trouble results from each person making only a few measurements, and different persons making different ones. A suggested standard has been offered (Norris, 1961) and use of it by all of us should in time advance us to a state of knowledge in which a key can be constructed to identify beaked whales in the flesh. Publication of just a total length of a specimen unqualified by a statement such as "measured personally in a straight line with tape" or "paced off" or "fisherman's estimate," results in seemingly scientific records of *Ziphius cavirostris* 7.6 and 8.56 m. long (Cabot, 1965, and Stephen, 1932, for example) which there is increasing reason to doubt as sets of measurements made with evident care by the naturalist or zoologist himself are showing no specimen longer than 6.58 m. (Kenyon, 1961, for example).

If there are rows of functional teeth on upper and lower jaws, but at the apex of the lower jaw there is a pair larger than any other and separated from the others by a gap larger than normal between the other teeth, it is *Tasmacetus.* If it has only four teeth near the apex of the lower jaw, the genus is *Berardius.* If it has only two flat (laterally compressed) teeth rising out of the lower jaw at some distance back from the apex of the jaw, it is a male of some species of *Mesoplodon.* If it has no teeth showing above the gum, it is either an immature or an adult female. To go beyond this, it is necessary to use the key to the teeth.

The best thing to do to be certain of identifying it, and of having a specimen in case it is of a rare species, is to carefully remove the head (with a sharp knife, never an ax or anything striking blows) and to mascerate it. This is best done for the smaller species in a 50-gallon steel drum located where the odor will disturb no one and dogs or other animals cannot get to it. Masceration may alternatively be

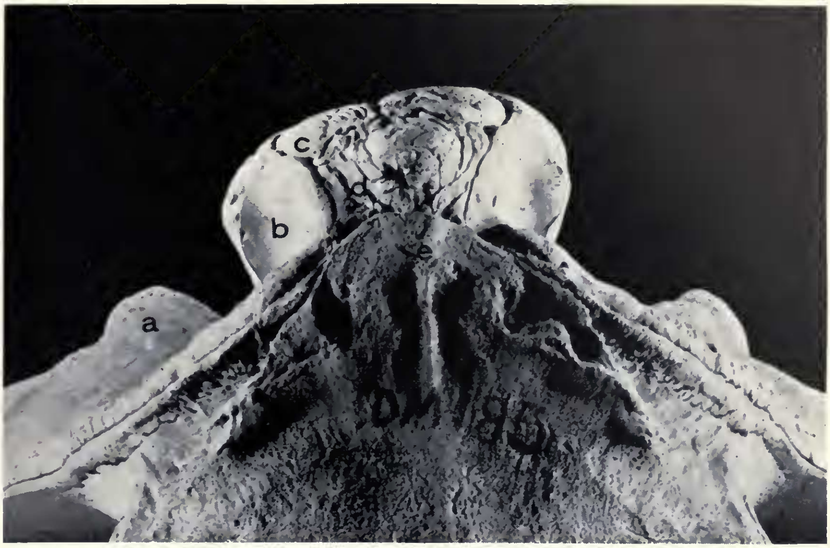

FIG. 23. Skull of *Berardius arnuxi*, posterior view. The elevated synvertex stands above the low supraoccipital showing sheer sides. The synvertex is slightly domed. Bones and bony features: left maxillary prominence (a), left maxillary (b), left nasal (c), divided left frontal (d), supraoccipital (e).

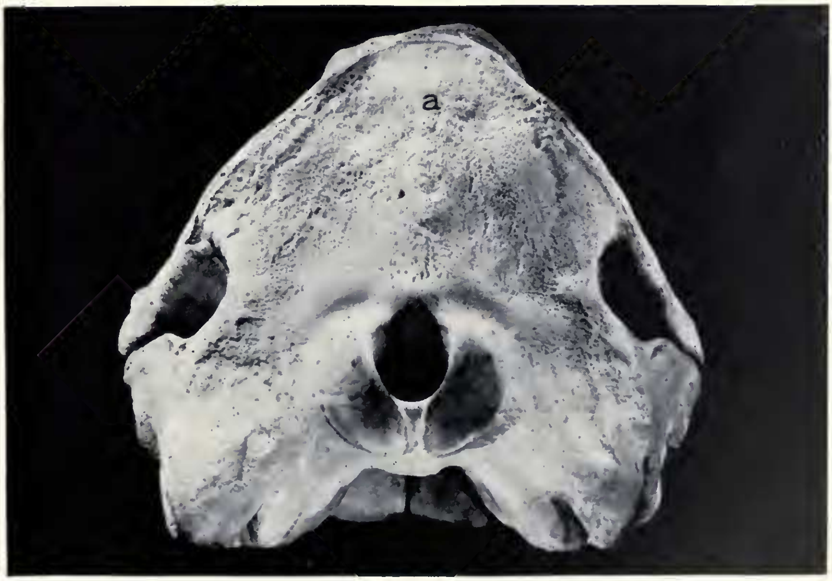

FIG. 24. Skull of *Ziphius cavirostris*, FMNH 99362, posterior view, on line with long axis of beak, illustrating how in the genera *Hyperoodon*, *Mesoplodon*, and *Ziphius* the high supraoccipital bone (a) shields the sheer sides of the elevated synvertex from posterior view. Compare with Figures 17 and 23.

accomplished by burial in the beach sand for several months some distance beyond high tide mark. The great risks one takes with this method are: 1) inability to devise a means of marking exactly where it is buried so that someone else will not remove the marker for another use; 2) likelihood that a storm will cut away that part of the beach, removing and losing the skull; 3) likelihood that the important teeth and earbones will be lost upon otherwise successful excavation of the cleaned skull.

KEY TO THE LIVING GENERA OF THE BEAKED WHALES BY CHARACTERS OF THE SKULL

(Applicable to adults, and probably most immatures[1])

1a. On the synvertex of the skull it is a nasal bone that extends farthest forward (as in Figs. 15 and 19) .... 2 (tribe ZIPHIINI)

b. On the synvertex of the skull it is a premaxillary bone that extends farthest forward (as in Figs. 13 and 16)..................3 (tribe HYPEROODONTINI)

2a. When the posterior aspect of the skull is viewed from a point aligned with the long axis of the rostrum, and from a distance of at least two meters, the profile of the synvertex projects above the supraoccipital as a slightly asymmetrical block with sheer sides (see Fig. 23)............................*Berardius*

b. When the skull is so viewed, the synvertex of it is completely occluded by the supraoccipital, or so little of the synvertex shows that the profiles of both descending sides are not seen to become sheer (see Fig. 24).........*Ziphius*

3a. A sulcus running along the middle of the combined surfaces of the pair of nasal bones, so depresses their combined middle anterodorsally that it is the lateral portion of each nasal bone which reaches farthest forward on the synvertex (see Figs. 13 and 16).........................5 (subtribe Hyperoodontina)

b. No such sulcus exists in the nasals (see Fig. 17)........................4

4a. The area of the synvertex of the skull occupied by the nasal bones far exceeds that occupied by the frontals (see Fig. 17)....................*Tasmacetus*

b. The area of the synvertex of the skull occupied by the nasal bones is less than or approximates that of the frontals.........................*Indopacetus*

5a. When the skull is upright and the long axis of the rostrum is horizontal, a horizontal plane touching the summit of the higher maxillary prominence (=crest), passes well above the mesethmoid bone (see Fig. 21)...*Hyperoodon*

b. When the skull is so oriented, a horizontal plane touching the summit of both (or the higher) of the maxillary prominences transects the mesethmoid bone (see Moore, 1966, figs. 6, 7)...............................*Mesoplodon*

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[1] By immatures in this instance I mean postnatal individuals with teeth not yet closed at the bottom, or with sutures of epiphyses on long bones or vertebrae not obliterated.

KEY TO THE LIVING GENERA OF BEAKED WHALES BY CHARACTERS OF THE TEETH OF ADULTS

1a. Some 20–27 well-developed teeth erupt on each side of the upper and lower jaws, each characteristically at least 15 mm. long and 5 mm. wide, and become worn...*Tasmacetus*

b. No teeth of such size become exposed through the gum, or no more than about four and restricted to lower jaw..2

2a. There are four well-developed teeth exposed through the gum close to the apex of the lower jaw (a larger apical pair and a smaller postapical pair, see Fig. 22) .... *Berardius*

b. There are no teeth erupted (as large as 15 by 5 mm.), or the number of such teeth is limited to two mandibular ones..............................3

3a. The two well-developed teeth (erupted, or cryptic beneath the gum) are compressed so that the greatest anteroposterior diameter of either tooth (perpendicular to the long axis of the tooth) is at least 1.66 of the greatest transverse diameter...*Mesoplodon*

b. The two well-developed teeth are substantially less flattened (i.e., more nearly round in cross-section)..4

4a. The two well-developed teeth are erupted and subject to wear in life (♂♂)..5

b. The two well-developed teeth do not erupt and wear (♀♀)................6

5a. The shape given the apex of the tooth by wear is fairly symmetrical and nipple-like (see Hale, 1931, fig. 11), suggesting that the central core of the tooth is harder than the peripheral parts (N=1).........♂ *Hyperoodon* (*planifrons*)

b. The shape of the worn surface is often strongly asymmetrical and not at all mammilate..7

6a. The cementum seems to invest the tooth only to within about a centimeter of the apex leaving exposed a slender, conical apex of dentine all around the base of which the cementum of the tooth immediately bulges (N=1, see McCann, 1961, pl. 3)................................ ♀ *Hyperoodon* (*planifrons*)

b. The diameter of the tooth *increases quite gradually* below the slender, conical, dentine cap of the apex..8

7a. The shape of the tooth is bulbous at the base but then becomes concave in profile as the girth of the tooth diminishes rapidly, then less rapidly, resulting in a delicately sinuous profile, as illustrated in Figures 5, 6, and 7. Its surface becomes wrinkled upon approach of adulthood. The wear, as illustrated in Figures 6 and 7, may be strongly oblique, the wear surface facing anterolaterally and upward . . . .♂ *Hyperoodon* (*ampullatus*)

b. The shape of the tooth is not bulbous at the base, and no concave profiles are normally formed by its growth and wear, and the cementum surface does not become wrinkled; the natural shape varies from that of a spindle in early adulthood almost to that of an egg at greater age. See Figure 5 lower right or consult Fraser (1942, pl. II, figs. f, g, h).........................♂ *Ziphius*

8a. The shape is basically conical, although the long axis bends dorsad; accretion at the base of the cone makes it somewhat bulbous there, and the surface of this becomes wrinkled (see Figs. 4 and 5); the ratio of greatest length of tooth to greatest transverse diameter exceeds 0.35............................ ....(subadult) ♀ *Hyperoodon* (*ampullatus*)

b. The basic shape is of a spindle, although gently bent dorsad and truncated proximally, and is illustrated in Figures 1, 5 lower left and lower middle, and 8 left; the ratio of greatest length to greatest transverse diameter is less than 0.32.. ♀ *Ziphius*

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SUMMARY

This paper is an outgrowth of an intensive revisionary study of the genus *Mesoplodon* which, after preliminary study of materials in North American museums (Moore, 1966), extended to collections on other continents. The most direct, and hence the best quantified, results in this present paper from the study of 292 skulls of beaked whales in 40 institutions, are the diagnoses of the genera, for it was to construct these that the observations presented in them were tabulated. From these, two dichotomous keys to the genera are derived, one by characters of the skull and one by those of the teeth.

The distinctions between the living genera of beaked whales, Hyperoodontoidea, had not been re-examined since the fifth living genus was discovered only 30 years ago, and the relationships between the living genera have never been investigated in a way that revealed sufficient evidence to provide a satisfying classification within the superfamily. With such a goal in mind I have here compared the genera as represented by 292 skulls of the 18 living species in two major lines of evidence, dentition and morphology of the elevated synvertex of the skull.

Separate comparisons and evaluation of the implications are offered here of: 1) the number and position of the teeth, 2) the size and shape of teeth, 3) the structure of the alveoli, 4) the morphology of the premaxillary crest, and 5) the shape of the nasals. All of these lines of evidence provide some information critical in assessing relationships, but those of the elevated synvertex, nos. 4 and 5, indicate the most inclusive groups. Using the morphological characters drawn from these five sources, a hypothetical phylogeny is constructed and presented as a dendrogram (Fig. 20) and a classification is offered based upon the postulated phylogeny.

New categories are recognized: tribes Ziphiini, including the genera *Berardius* and *Ziphius;* and Hyperoodontini, including genera *Tasmacetus, Indopacetus, Hyperoodon,* and *Mesoplodon;* subtribes Berardiina and Ziphiina to contain their respective genera *Berardius* and *Ziphius,* because they have diverged from each other more markedly than generic degree of difference but less than tribal degree;

Tasmacetina, to include *Tasmacetus* and to indicate the greater than generic but less than tribal differences between it and Hyperoodontina which includes the genera *Hyperoodon* and *Mesoplodon*. The two species of *Hyperoodon* are elevated to subgeneric level, and the new name required for this is *Hyperoodon* (*Frasercetus*) *planifrons*.

A preliminary classification of the species of *Mesoplodon* is presented, derived from relationships between number, position, and morphology of the teeth, and recognizing monotypic subgeneric status for two. The species *pacificus* is removed from the genus *Mesoplodon* and elevated to generic rank, *Indopacetus*, new name, with subtribal status to indicate the degree of its distinction from the polytypic *Hyperoodontina*.

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